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THE ENTOMOSTRACA OF THE WEEDS OF A MOORLAND POND

BY W. J. P. SMYLY

Freshwater Biological Association, Ambleside

(With 3 Figures in the Text)

Wise Een Tarn (Nat. Grid Ref. 34/370975) lies on Claife Heights, a low range of hills to the west of Windermere, at an altitude of 650 ft. (199 m.). It is surrounded by typical moorland vegetation and was made by the building of a dam about 1900. Its surface area is 52,700 sq. yd. (44,500 sq.m.), its maximum depth, near the outflow is about 10 ft.; over much of its area the depth does not exceed 3 ft.; as no survey of the tarn has been made, these depth figures are only approximate. Two streams flow into it; one enters at the south-east corner and drains a neighbouring pond, Scale Tarn; the other drains high ground to the south-west of the tarn and enters it on the side opposite to the dam. In the summer and winter of 1947 the alkalinity (as mg. $CaCO_3$/l.) was 9·0 and 6·6 respectively; the corresponding calcium concentrations were 4·9 and 3·7 mg./l. No survey of the rooted aquatic vegetation has been made; the common water plants were *Carex rostrata*, *Equisetum fluviatile*, *Potamogeton natans* and *Juncus bulbosus* forma *fluitans*.

In summer, the water-level often fell appreciably, but the extent of the fall was not measured; in winter, the tarn was usually frozen over for a few weeks at least. Between April and October, collections were made at weekly intervals, but in the winter months when few animals were caught, intervals of 3 or 4 weeks separated the sampling dates. Twelve tow-nettings were made in mid-tarn between March and June 1950 for comparison. At each visit, the water temperature was taken and general weather conditions were noted. Forty-two collections (between April 1949 and June 1950) were made at five marginal stations selected so that all weed-beds would be sampled. These five stations are shown in Fig. 1 by Roman numerals. *Carex* was common at all five stations, and because it grew nearest the water edge was generally completely exposed during dry periods in summer. Offshore the emergent stems of *Equisetum* and the floating leaves of *Potamogeton* were the characteristic features of each weed-bed, except at Station V where there was no *Potamogeton*. At both Stations I and IV a bed of *Equisetum* overlapped somewhat with an adjoining bed of *Potamogeton*; at Station II *Equisetum* was more abundant than at Stations I and IV, and formed a thick fringe enclosing and encroaching on a rather small amount of *Potamogeton*; at Station III *Potamogeton* was more abundant than at any other station and was screened by a thin fringe of *Equisetum* on its border nearest the open water of the tarn. *Juncus bulbosus* was not abundant except at Station V where *Equisetum* was as abundant as at Stations I and IV. Taking the depth to which the human leg sinks in as a rough measure of the amount of detritus at each station, Station II had more detritus than

any other, and Stations I, III and IV each had a similar covering of detritus. Station V had a bottom of coarse silt.

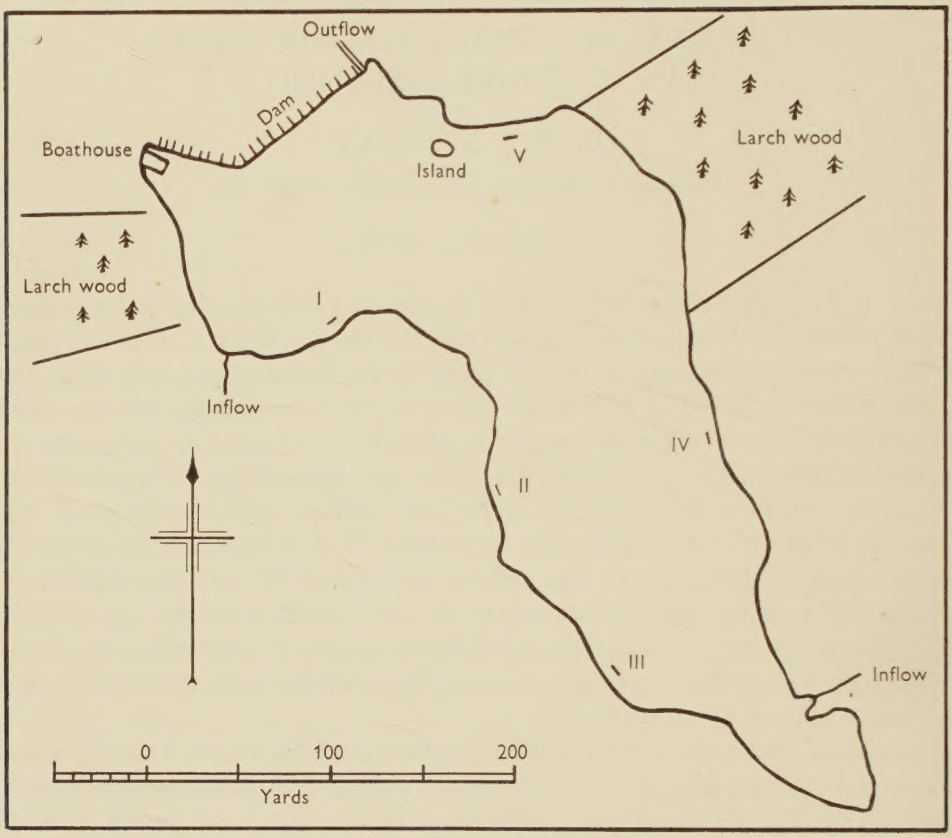

Fig. 1. Sketch map of Wise Een Tarn to show the positions of the five collecting stations.

METHODS

In weed-beds nets and pumps are impracticable; nets clog rapidly even in open water (Ricker 1932), and an efficient pump requires a motor. The grab used by Macan (1949) was therefore tested as a means of catching weed-dwelling Entomostraca. This grab is a metal box with two fixed and two hinged sides. When the hinged sides are apart, the opening at the bottom encloses an area of 0·1 sq.m. The bottom is closed by bringing the hinged sides together. The volume of the grab when closed is 31·5 l. The top and sides of the grab have holes to allow water to run off. In order to retain weed Entomostraca, these holes were covered with no. 60-mesh bolting silk. Tests showed that the grab was easy to handle and caught enough animals.

The sampling error of the grab was found by taking six grab hauls at the same time and place, examining each sample separately, and analysing the results statistically. This analysis showed that, with the exception of *Polyphemus pediculus*, the variation in numbers of species in replicate samples was not large and could be described by a Poisson distribution, for which the tables calculated by Ricker (1937) give 'confidence limits' for numbers of animals from 0 to 200. Reference to these tables showed that

only rather large differences in abundance were statistically significant, e.g. between 0 and 40, 40 and 110 and 110 and 215.

A thin layer of the bottom was removed in each grab sample because some bottom debris helped to seal the jaws of the grab and some Entomostraca are known to be detritus feeders. Three grab samples were taken in each weed-bed. More would have given a small increase in accuracy incommensurate with the extra time spent in examining the samples; also the weed-bed was considerably disturbed each time a grab sample was taken. Grab collections were placed in fine-mesh bags which allowed water to drain through but retained everything else. The contents of each bag were washed into a large enamel dish. Large pieces of plant were rinsed and picked out with forceps. If there was much mud, the sample was strained through a sieve which retained Entomostraca, but let smaller particles pass through. When as much debris as possible had been removed, the sample was concentrated by filtering off excess water through a zooplankton net. Formalin (5%) was then added and the volume made up to 300 ml.; 25 ml. were removed with a Stempl pipette in five fractions of 5 ml. each. Before the removal of each fraction, random distribution of the organisms was obtained by shaking the bottle as described by Worthington (1931). The organisms were counted in a trough under low magnification (Ullyott 1937). All *Cyclops* species and some Cladocera were identified under higher magnification.

RESULTS

Thirteen species of Cladocera and six species of Copepoda were found amongst the marginal weeds of the five weed-beds studied. Five of the thirteen species of Cladocera and one of the six Copepoda were always rare both in quantity and frequency of occurrence and will not be considered further. From the fact that seven of the thirteen common weed species were caught in mid-tarn, it is evident that no clear-cut distinction exists in ponds between the open water and the marginal zone.

Table 1 shows the total numbers of each species and the collective totals of the numbers of all species at each station from April 1949 to April 1950. Most weed Entomostraca were caught at Station II and fewest at Station V. The differences between the total numbers at these two stations and those at Stations I, III and IV were statistically significant. Any attempt to assess the significance of these differences must clearly be preceded by an examination of the species composition of the totals. An interesting preliminary step is the separation of species confined to the weeds from species found also in the open water.

Twelve surface tow-nettings were made in mid-tarn. The names, totals, and relative abundance (%) of species which were caught by tow-netting are shown in Table 2. In March, *Diaptomus gracilis*, *Chydorus sphaericus* and *Cyclops leukartii* were the common species, but by mid-April, only *Diaptomus gracilis* was present in large numbers. Early in May, *Daphnia longispina* and *Polyphemus pediculus* appeared. The latter soon disappeared and was replaced by *Ceriodaphnia pulchella* at the end of May. In early June, *Daphnia longispina* was more abundant than *Ceriodaphnia pulchella*, but towards the end of the month they were equally abundant. Because no mid-tarn collections were made after June, the list of species in Table 2 may be incomplete.

Comparison of mid-tarn and weed collections showed that *Daphnia longispina* was

never caught amongst weeds, and *Cyclops leukartii* only rarely, but *Diaptomus gracilis*, *Polyphemus pediculus*, *Ceriodaphnia pulchella* and *Chydorus sphaericus* were all abundant at times in the weed-beds.

Table 1. *Totals of weed Entomostraca*

Each figure is the sum of the mean number of the species in one grab haul (30 litres) on each collecting day.

Organism	No. of times recorded	Station I	II	III	IV	V
Diaptomus gracilis Sars*	31	1302	1265	976	596	424
Cyclops viridis (Jurine)	31	494	476	336	524	370
Eurycercus lamellatus (O. F. Müller)	29	320	237	312	380	298
Cyclops albidus (Jurine)	28	312	392	284	228	152
Drepanothrix dentata (Euren)	26	216	748	438	212	72
Cyclops macruroides s.s. Lilljeborg	23	288	580	404	324	316
Cyclops agilis Koch, Sars	22	180	64	128	132	76
Sida crystallina (O. F. Müller)	19	300	271	428	672	132
Ceriodaphnia pulchella Sars*	18	470	687	1100	1284	324
Chydorus sphaericus Baird	18	2388	5731	2146	1276	184
Peracantha truncata (O. F. Müller)	17	364	76	348	420	48
Polyphemus pediculus (Linn.)*	16	248	404	164	438	76
Alona affinis (Leydig)	15	40	40	84	24	24
Chydorus globosus Baird	4	8	4	16	24	8
Ilyocryptus sordidus (Lieven)	2	8	0	0	0	0
Cyclops leukartii Claus	2	4	16	21	16	0
Acroperus Harpae Baird	1	12	4	0	40	0
Graptoleberis testudinaria (Fischer)	1	0	0	0	4	0
Simocephalus exspinosus (Koch)	1	0	28	0	0	0
Totals		6954	11,023	7183	6594	2504
Ratio of totals		2·8	4·4	2·9	2·6	1·0

* Common in open water and weeds

Table 2. *Mid-tarn Entomostraca*

Totals and percentages (in italics) of the species taken near the surface in open water.

	Diaptomus gracilis		*Polyphemus pediculus*		*Ceriodaphnia pulchella*		*Daphnia longispina*		*Chydorus sphaericus*		*Cyclops leukartii*		Other species	
7 Mar.	70	*63*	0	*0*	0	*0*	0	*0*	12	*11*	27	*24*	3	*2*
29 Mar.	34	*20*	0	*0*	0	*0*	6	*4*	80	*46*	44	*25*	8	*5*
13 Apr.	43	*45*	10	*11*	0	*0*	0	*0*	23	*24*	19	*20*	0	*0*
18 Apr.	356	*97*	0	*0*	0	*0*	8	*2*	0	*0*	2	*1*	0	*0*
4 May	270	*90*	0	*0*	0	*0*	25	*8*	0	*0*	6	*2*	0	*0*
9 May	198	*85*	21	*8*	0	*0*	15	*6*	0	*0*	1	*1*	0	*0*
17 May	300	*80*	42	*11*	0	*0*	36	*9*	0	*0*	0	*0*	0	*0*
23 May	51	*18*	134	*48*	0	*0*	94	*34*	0	*0*	0	*0*	0	*0*
31 May	21	*16*	65	*50*	9	*7*	15	*12*	16	*12*	4	*3*	0	*0*
7 June	3	*2*	6	*4*	31	*22*	92	*66*	0	*0*	7	*5*	1	*1*
13 June	8	*2*	3	*1*	59	*15*	324	*80*	0	*0*	4	*1*	9	*2*
28 June	20	*5*	0	*0*	201	*47*	197	*47*	0	*0*	5	*1*	0	*0*

On the available data then, the animals can be grouped as follows:

Common in open water:

(*a*) Not found in weeds — *Daphnia longispina* O. F. Müller
(*b*) Rare in weeds — *Cyclops leukartii* Claus
(*c*) Common in weeds — *Diaptomus gracilis* Sars
Polyphemus pediculus (Linn.)
Ceriodaphnia pulchella Sars
Chydorus sphaericus Baird

Common in weeds:

(*a*) Uncommon in mid-tarn
Eurycercus lamellatus (O. F. Müller)
Cyclops viridis (Jurine)
Cyclops albidus (Jurine)

(*b*) Not found in mid-tarn
Cyclops agilis Koch, Sars
Cyclops macruroides s.s. Lilljeborg
Sida crystallina (O. F. Müller)
Peracantha truncata (O. F. Müller)
Drepanothrix dentata (Euren)

Rare in open water and weeds:

Simocephalus exspinosus (Koch)
Acroperus harpae Baird
Chydorus globosus Baird
Ilyocryptus sordidus (Lieven)
Graptoleberis testudinaria (Fischer)

This grouping shows that of fourteen Entomostraca common in the tarn, eight species were found in both open water and weeds, five species only in weeds and one species only in the open water.

Daphnia longispina was the one species which occurred abundantly in mid-tarn but was never taken amongst weeds. In lakes it is a pelagic species. It would be expected therefore that it would be rare in marginal weeds of a pond, but its complete absence there is rather surprising. *Ceriodaphnia pulchella* which closely resembles *Daphnia* in structure but is a smaller animal, was equally common in both weeds and open water. No explanation of these differences in behaviour can be given. Of the five species which were found only in weed-beds, only *Sida crystallina* has a special means of attachment, a gland on the back of its head.

Of the four species which were common in mid-tarn and also in the weeds, one, *Chydorus sphaericus*, was relatively abundant (46%) on only one occasion, and that occasion was before its seasonal maximum in the weeds. But the other species (*Diaptomus gracilis*, *Polyphemus pediculus* and *Ceriodaphnia pulchella*) were abundant in mid-tarn during the time when they were common in the weeds. The collective totals of these three latter species are shown in Table 3. From the ratios given in the

Table 3. *Collective totals of Entomostraca and ratios (to Station V as unity)*

	Station				
	I	II	III	IV	V
A. Species common in both open water and weeds	2020	2356	2240	2318	824
	2·5	2·9	2·7	2·8	1·0
B. Species common in weeds but scarce in open water	4934	8667	4943	4276	1680
	2·9	5·2	2·9	2·5	1·0
Ratio B:A	2·4	3·7	2·2	1·8	2·0

bottom line, it is evident that the large total at Station II results from relatively more weed than open-water species at this station, because at the other four stations, the ratio of open-water to weed species is of the same order, 1 : 2 in each instance. It is clear also from the ratios given in the second and fourth horizontal lines that the small total at Station V results from a relative scarcity of both the planktonic and the weed species.

Although their collective totals were similar at Stations I–IV, individually *Diaptomus*, *Polyphemus* and *Ceriodaphnia* showed differences in their distribution. *Diaptomus* was

more abundant at Stations I–III than at IV or V; *Ceriodaphnia* was more abundant at Stations III and IV than at I, II or V; *Polyphemus* was more abundant at Stations I, III and IV than at either II or V. The largest numbers of *Diaptomus* were found on windward shores, but no relationship of this kind was found for either *Polyphemus* or *Ceriodaphnia*. Even on calm days, any one of the three species might be found in great abundance in one or more weed-beds and might be scarce or absent in others. Chance probably plays a large part in the distribution of these three species, although the fact that all three species were scarce at Station V, where the lowest total of all

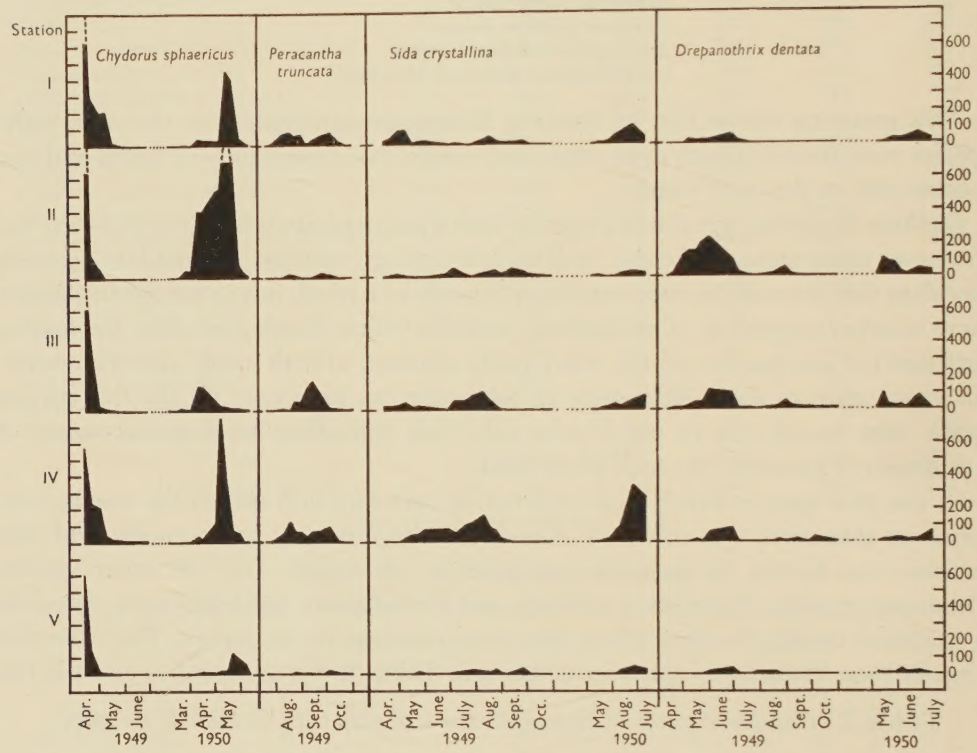

Fig. 2. Seasonal maxima of four species of weed Entomostraca which showed statistically significant differences in their relative abundance at the five stations.

species collectively was recorded, may have some significance. The weed-dwellers collectively were five times more numerous at Station II and nearly three times more numerous at Stations I, III and IV than at Station V. Table 1 shows that these numerical differences were due to differences in total numbers of only a few species. Individually, the most abundant of these few species was *Chydorus sphaericus* which was twice as abundant at Station II (where it formed more than half of the total numbers of all Entomostraca) as it was at Stations I, III and IV, and over thirty times as abundant as at Station V (Fig. 2). Statistically, the differences between the totals of *C. sphaericus* at all stations (except between those at Stations I and III) were significant. Some significant differences between totals at different stations were shown also by *Drepanothrix dentata*, *Peracantha truncata* and *Sida crystallina* (Fig. 2),

but none of the remaining species were significantly more abundant at any one station than at another.

The observed differences in the collective totals of Entomostraca at each station have now been accounted for in terms of individual species. In a preliminary work of this nature, however, a full explanation of the ecology of each species cannot be attempted. The element of chance is always present, and its influence on results is not easy to assess. Nevertheless, there are some points of interest in the data which appear to have some significance. The relative scarcity of all Entomostraca, both of the

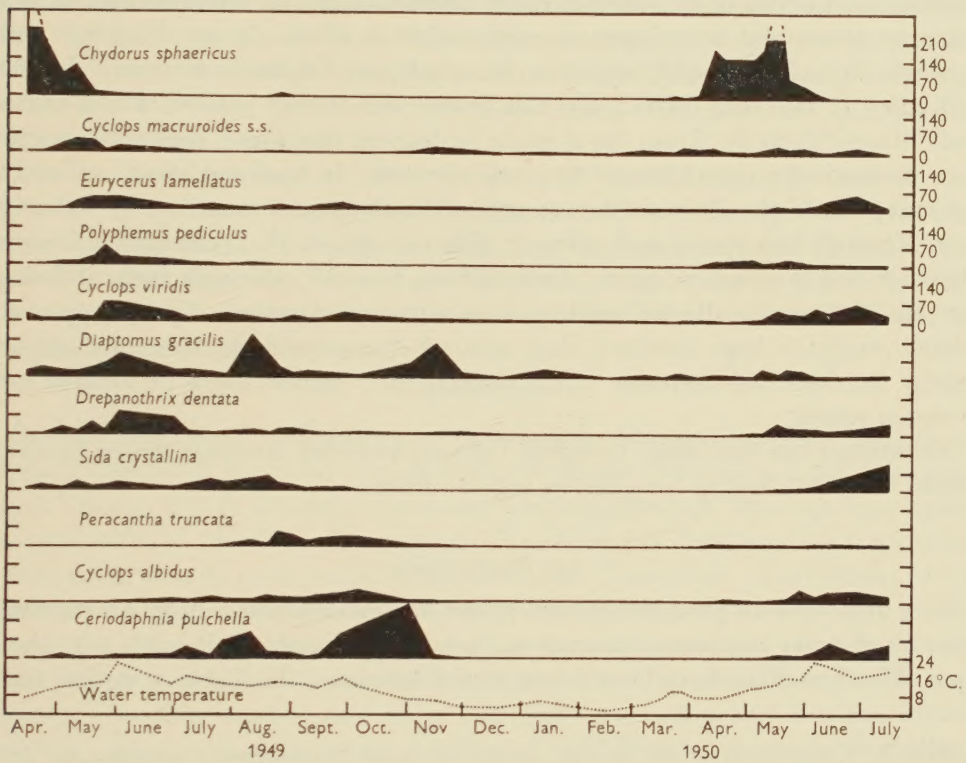

Fig. 3. Seasonal changes in abundance (April 1949 to July 1950) of the common weed Entomostraca. The numerical values, on which each graph is based, represent the averages of fifteen grab samples, three at each of the five stations.

planktonic kinds and the true weed-dwellers, at Station V is more than a chance result. The scarcity of weed species at this station is clearly associated with the scarcity of weeds, notably *Potamogeton*, but neither this factor nor the silted nature of the bottom seems adequate to account for the relative scarcity of the planktonic species also. Local distribution of four weed-dwelling species has been noted as significant. Two of these species, *Chydorus sphaericus* and *Drepanothrix dentata*, show an apparent correlation between their relative abundance and the amount of detritus and vegetation at each station, but the other two, *Sida crystallina* and *Peracantha truncata*, show no such correlation. The latter species was most abundant in those weed-beds where *Potamogeton* was plentiful and, in some measure, this association is true also of *Sida crystallina*. In view of these four examples of local distribution of weed-dwelling

species, it is at first sight curious that the remaining species appear to be distributed at random, but this apparent uniformity may in fact be illusory and be mainly a consequence of the rather crude sampling technique.

In Fig. 3 seasonal changes in abundance of each species are shown as graphs based on mean values calculated by dividing the sum of the daily totals at each station by the number of stations. The consequence of this procedure is that only large differences in number (between 0 and 40, 40 and 110, and 110 and 215) have any significance statistically, but it achieves the purpose of depicting in broad outline the seasonal maxima and minima of the weed-dwelling Entomostraca. In winter all species were scarce or absent and only Copepoda were caught as adults. In late March or early April the first of the weed Cladocera to be caught was *Chydorus sphaericus*. In 1950 collections in mid-tarn showed that this animal was already present in mid-tarn in early March (Table 2). From this it might be deduced that winter eggs of this species hatch first in mid-tarn and later in the marginal weeds. In April and May *C. sphaericus* was exceptionally abundant and then disappeared until the same months of the following year. Through the spring and summer different species of Entomostraca became abundant and grew scarce again. *Ceriodaphnia*, however, although fairly abundant through the summer, did not reach its maximum until October. *Cyclops* spp. were seldom present in large numbers; their seasonal changes took the form of slight but regular increases and decreases which reached their highest levels in summer and lowest in winter.

No attempt has been made to survey the very scattered literature on the fauna of ponds, but the following comparisons may be drawn.

(*a*) *Productivity*

Very little work on pond Entomostraca with apparatus which samples a measurable quantity of water has been attempted and no results directly comparable with those from Wise Een Tarn have been found in the literature. In Table 4, figures from

Table 4. *Comparison of the largest number of weed Entomostraca recorded per litre from* (*a*) *the lake of Fredericksborg Castle* (*Berg & Nygaard* 1929) *and* (*b*) *Wise Een Tarn*

	(*a*)	(*b*)
Bosmina longirostris	952	Absent
Chydorus sphaericus	355	120
Daphnia cucullata	229	Absent
Diaphanosoma brachyurum	25	Absent
Cyclops strenuus	67	Absent
C. viridis	Absent	5
Diaptomus graciloides	65	Absent
D. gracilis	Absent	19

Berg & Nygaard (1929), who trapped Entomostraca in the open water of a Danish lake, are shown for comparison with figures from Wise Een. When a Danish species is absent from Wise Een but another species of the same genus is present, figures for the latter species are given in the table. The disparity between the figures reflects the difference in the quality of water in a moorland tarn and a highly eutrophic lake.

(*b*) *Species composition*

Species lists of weed Entomostraca which have been based on collections made at frequent intervals through the year are scarce in the literature. None have been found for these islands and only a few for other countries. Among the latter, the papers of Lilljeborg (1900), Nordquist (1921), Berg (1929), Ward (1940) and Sebestyen (1948) have been consulted. Comparison of the species found in Wise Een Tarn with those found in Scandinavia, America and Hungary shows that the majority of weed Entomostraca are common in all the waters studied. In Sweden, Nordquist (1921) has listed the Entomostraca which are characteristic of waters of different size (pools, ponds and lakes) and has also classified ponds as oligotrophic or eutrophic according to their Entomostraca. On Nordquist's classification, Wise Een Tarn resembles an oligotrophic Swedish pond.

Two common members of the weed fauna in Scandinavia and America, viz. *Bosmina longirostris* and *Diaphanosoma brachyurum*, were not found in Wise Een. The former is uncommon in Lake District tarns, but the latter was found abundantly in an isolated collection from Three Dubs Tarn barely a mile distant from Wise Een. The absence of *D. brachyurum* may have an ecological explanation which will be discussed in the next section.

(*c*) *Ecology*

Daphnia longispina is well known to be pelagic in lakes and scarce in margins of ponds (Ostenfeld & Wesenberg-Lund 1905; Nordquist 1921; Berg 1929; Sebestyen 1948). The fact that *D. longispina* was absent from weed-beds in Wise Een Tarn agrees therefore with the results of other workers. The absence of *Diaphanosoma brachyurum* is interesting because it occurs in the open water of Three Dubs Tarn (Macan 1949). However, no weed collections were made in Three Dubs and results from abroad (Nordquist 1921; Berg 1929) show that *D. brachyurum* is pelagic and usually very scarce in weedy margins. It is uncertain whether or not the animal occurs in the open water of Wise Een because open-water collections were taken only between March and June. Association of the largest numbers of weed Entomostraca with the thickest submerged and emergent vegetation in Wise Een is in agreement with the findings of other workers (Mackay 1924; Bajkov 1929; Entz 1946).

No authors have been found who associate *Chydorus sphaericus*, *Drepanothrix dentata* or *Peracantha truncata* with any particular kinds of habitat, but there are references in the literature to *Sida crystallina* and other species of Entomostraca in relation to particular water weeds. *S. crystallina* has been found abundantly on *Sparganium minimum* (Gurney 1928) and *Potamogeton perfoliatus* (Entz 1946; Langhans 1911); *Acroperus harpae* on *Myriophyllum spicatum* (Entz 1946); *Eurycercus lamellatus* and *Simocephalus vetulus* on Chara sp. (Gurney 1928).

(*d*) *Seasonal differences*

The seasonal changes in abundance of weed Entomostraca in Wise Een Tarn are similar to those which take place in ponds in Europe and America, e.g. in Swedish ponds, Cladocera were dominant from May to September, but in winter there were

only Copepoda (Nordquist 1921). The seasonal occurrence of individual species in Wise Een is similar to that in other ponds, with one main exception. *Chydorus sphaericus* was abundant in Wise Een in April and May but was scarce or absent in all other months. Lilljeborg (1900), however, found it all through the year even under ice in December. Sebestyen (1948) found it in all months except January and February. Ward (1940) made the interesting observation that in Cincinnati ponds *C. sphaericus* was absent in winter in shallow ponds but present all through the year in deeper ponds. Neither Lilljeborg nor Ward give any indication of numbers; they simply note the presence or absence of the species. It is possible therefore that more thorough search in Wise Een Tarn would have yielded small numbers of *C. sphaericus* through all the warm months of the year, and even perhaps in deeper water in winter. If this were so, Ward's observation would suggest an explanation of the occurrence of *C. sphaericus* in the open water of the tarn in March before it had been found in the weed-beds.

ACKNOWLEDGEMENTS

I am greatly indebted to Dr T. T. Macan and Mr H. C. Gilson for their criticisms of this paper and their suggestions on its presentation.

SUMMARY

1. A quantitative study has been made of the Entomostraca of the weed-beds of an artificial moorland pond situated at 650 ft. (199 m.) on Claife Heights, a low range of hills to the west of Windermere.

2. Collections of weed Entomostraca were made with a special type of hand-grab at weekly intervals through the year from five stations chosen so that all weed-beds would be sampled. A few mid-tarn collections with a tow-net were made for comparison.

3. Thirteen species of Cladocera and six species of Copepoda were found, but only seven of the former and five of the latter were common in weed-beds.

4. Largest numbers of weed Entomostraca were caught where vegetation was thick and the bottom covered with organic detritus (Station II) and smallest numbers where vegetation was sparse and the bottom silted (Station V).

5. Comparison of mid-tarn and weed collections showed that six species were relatively abundant in mid-tarn. Of these six species: *Daphnia longispina* was never found in weeds; *Cyclops leukartii* was very rare in weeds; *Chydorus sphaericus* was only once abundant in mid-tarn and was so before its seasonal maximum in the weeds. Only *Diaptomus gracilis*, *Polyphemus pediculus* and *Ceriodaphnia pulchella* were present in open water and weeds concurrently.

6. The small total of all species at Station V resulted from a relative scarcity of both planktonic and weed species, whereas the large total at Station II resulted from a relative abundance of weed species, especially *Chydorus sphaericus*.

7. Four weed species showed localized distribution. *Chydorus sphaericus* and *Drepanothrix dentata* were more abundant where vegetation and detritus were plentiful; *Peracantha truncata* and *Sida crystallina* were most abundant in those weed-beds where *Potamogeton natans* was plentiful.

8. Seasonal changes in abundance were shown by all species. Adult Cladocera were absent in winter; only Copepoda were found as adults in all months. The typical seasonal cycle of Cladocera was a short period of considerable abundance followed by a long period of scarcity, whereas Copepoda were typically present in rather small numbers for quite long periods.

9. Comparisons with ponds in other parts of the world show that in respect of its Entomostraca, Wise Een Tarn is a typical oligotrophic pond.

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THE STRUCTURE OF A DENSE NATURAL ANT POPULATION

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(With 3 Figures in the Text)

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INTRODUCTION

The importance of ground insolation to ant growth in the west of Scotland has already been demonstrated (Brian & Brian 1951). In two subseral vegetation sequences ant population at first rose and then fell as the growing vegetation reduced the insolation quota reaching the soil surface. Either of these subseres, that following heather-burning, or that following the felling of woodland, may be arrested—usually locally—by mammalian grazing and browsing, in which case short grass-heath (acidic *Festuca-Agrostis* grassland) results. As this is comparatively stable, with insolation reaching within a few centimetres of the soil, and as the mammals (roe-deer, sheep, hares, rabbits and voles principally) are usually not sufficiently heavy-footed or dense enough to trample the nests seriously, high ant population-densities may be attained. In the woodland type of plagioclimax, where stumps are available as nest-sites, all four species of ant typical of such situations in the uplands of Britain, *Formica fusca* L., *Myrmica scabrinodis* Nylander, *M. rubra* Nylander (the form *macrogyna* Brian & Brian 1949 only) and *Leptothorax acervorum* Fabricius become well established. In this paper the distribution is described and some of the determining factors are analysed.

THE HABITAT

The trees, species of *Pinus*, had been felled some 28 to 30 years before this investigation, and there had since been little interference with the area by man, apart from the digging of a few drainage channels and periodic rabbit shooting. No attempt was

made to replant. From the size of the stumps, 0·5–0·75 m. in diameter, it was evident that the wood had been allowed to mature before felling, and that the trees at this time were of considerable size. The stumps, as would be expected in such a woodland, were irregularly disposed at some 5–10 metres apart, and had reached an advanced state of decay and erosion; the bark had been torn away or buried, the wood was well rotted at the periphery and centre, and where soft had been eroded to varying degrees by rabbits (*Oryctolagus cuniculus*) and woodpeckers (*Dryobates major*). The axe-cut part of the stump with an irregular surface had been overgrown by the general soil biota, but the higher, smooth, and near-horizontal saw-cut part was still only lichen and alga covered with rarely a little moss.

Between the stumps the ecosystem, developed on a sticky glacial boulder clay, was in spite of the efforts at drainage a mosaic of high-dry and low-moist areas. The high-dry areas were only 30 cm. at the most above the others, and were usually around the tree stumps to which they clearly owed their elevation. They showed about 10 cm. of acid (pH = 4·5–5·0) humus-rich soil overlying a pale straw-coloured sand about 20 cm. in thickness (pH = 5·0–5·5) which in turn lay on the parent drift. The vegetation consisted of *Polytrichum* spp. (d.), with *Rumex acetosella* (f.) and *Festuca ovina* (f.) as its principal associates.* This type of ecosystem may be found around the bases of large pine trees before felling, and is for the most part a relict of the woodland conditions—possibly the soil-form more so than the present vegetation.

The lower areas were waterlogged in wet weather but frequently dried out, especially in early summer which is a relatively dry season. Above the drift the soil was a fairly homogeneous unstratified grey colour with pH rising from 5·5 near the surface to 6·0 below, and containing many worms (Lumbricidae) and moles (*Talpa europea*). The vegetation was very mixed: *Succisa pratensis* (f.), *Juncus conglomeratus* (f.), *Cirsium palustre* (o.), *Anthoxanthum odoratum* (o.), *Carex* spp. (o.), *Potentilla erecta* (o.). Where these two extreme types of ecosystem blended, the vegetation characteristically consisted of: *Agrostis tenuis* (f.), *Galium saxatile* (f.), *Potentilla erecta* (f.), *Luzula campestris* (o.), *Lonicera* sp. (o.), *and Succisa pratensis* (o.). The creeping *Galium* and *Potentilla* tended to encroach on to the *Polytrichum*-dominated areas, and this and other evidence suggested that the latter were slowly diminishing in extent. Birches (*Betula* sp.), isolated or in groups of two or three, were sparsely distributed over the whole area, and ranged in height from 1 m. to 4 or 5 m. The distance apart averaged about 5 m., and together with a dense plantation of conifers to the south, these provided an effective wind-break.

The principal grazing animal was the rabbit, and the herbs inside exclosures grew rapidly. The roe-deer (*Capreolus capreolus*) was second in importance, but its effects were not assessed. Voles (Microtinae) were not in evidence and certainly had no effect on the vegetation at the time of study. Farm animals never had access to the area. Such a habitat, largely free from human interference, exposed to sunlight, protected from wind, moderately grazed to allow the sun to reach near to the soil surface, and by light-footed animals to minimize nest destruction, with a moisture gradient,

* The method of describing plant frequency is that used by Tansley (1939) as is also the general terminology. The names of plants conform with the check-list of Clapham (1946).

rotting stumps as well as turf to nest in, and a rich variety of herbs to foster a varied food supply, provides the best conditions in the west of Scotland for the growth of ant populations.

THE DISTRIBUTION OF NESTS

(*a*) *The stump and off-stump populations*

For this comparison thirty stumps and thirty yard squares taken randomly within 3 yd. of each stump were examined for nests. Stump and associated off-stump quadrat could thus be grouped as a pair if necessary in the analysis. Quadrats were never taken on the extreme low-moist *Juncus-Succisa* ecosystems as these were known to be unsuitable for ant nesting. The salient points that emerged from this survey may be summarized as follows:

(1) The ratio *fusca* : *scabrinodis* : *rubra* : *acervorum* was 23 : 20 : 12 : 7 on stumps, and 1 : 13 : 18 : 1 off stumps. In the latter habitat therefore *rubra* predominated, *fusca* and *acervorum* were conspicuously less frequent, and *scabrinodis* still plentiful. On the stumps, on the other hand, *fusca* and *scabrinodis* predominated and *acervorum* was common.

(2) The frequency with which 0, 1, 2, 3, 4 and 5 nests per sample were experienced was 0, 10, 11, 6, 3 and 0 respectively on-stumps, and 7, 15, 6, 2, 0 and 0 off-stumps. Since the mean numbers of nests per sample were thus 2·1 and 1·1 respectively, it can readily be seen that both agree in having less empty quadrats and more with one or two nests than would be expected if the nests were distributed at random in the areas sampled. The statistical significance of this possible over-dispersion cannot be tested, however, as the data are insufficient.

(3) Nests on the stumps were large as a rule. This was especially true for *fusca* with 21 large and 2 medium nests;* *scabrinodis* had 15 large, 4 medium and 2 small; whilst *rubra*, with 6 large, 2 medium and 4 small, had the smallest average nest size. Thus, if it were practical to consider the total populations without destroying them, the differences in species frequency already found as regards nest number would be further accentuated. A few queen foundresses were found, two *fusca* and one *rubra*, so that attempts at colonization continued in spite of an already high population density.

There are interesting differences between this population and that of the unimpeded subsere (Brian & Brian 1951). In the latter 12 years after felling there was an average of 2·5 nests per stump (these were of similar size), and in the off-stump areas suitable for colonization the average area per nest was 3·75 sq.yd. Thus the plagioclimax figures of 2·1 per stump and 0·91 sq.yd. per nest off-stumps suggest that a movement from the stumps to the surrounds had taken place. The species proportion on unimpeded subsere stumps was (in the order used above and throughout this paper) 6 : 4 : 12 : 3, and off-stumps 0 : 3 : 2 : 0. Thus whilst the off-stump population could be similar in both habitats, the stump population clearly differs, there being relatively less *rubra* in the plagioclimax. The data thus suggest that as a result of the interference by mammals in the normal vegetational sequence and the consequent development

* Mature nests with sexuals are called large, nests with 100 workers or less, small, and nests of intermediate sizes, medium. This classification was used in an earlier paper (Brian & Brian 1951), and is not intended as a means of comparing the nest size of different species, but merely as a rough guide to the maturity of the nests of a particular species.

of a relatively stable ant-inhabitable ecosystem, there has been time for the *rubra* component of the population to be partially removed in some way from the stumps.

The sparsity of both *fusca* and *acervorum* off-stumps, can probably be explained by the fact that both these are gallery-making but not mound-making ants. Their method of obtaining access to insolation heat, whilst maintaining high humidity and darkness for their brood, is to gallery under bare soil or in wood, not to erect 'solaria' as the two *Myrmica* species do. On the occasions when they were found off-stumps, it was under short moss or the bare soil of a ditch-side. In this locality *fusca* with few exceptions (and these small colonies) nests under stones, in stumps and logs, or under bare soil. *Leptothorax acervorum* may also nest in rock crannies; in moorland both nest in lichen-covered peaty soil. Thus in the plagioclimax of felled woodland both are almost entirely dependent on the old stumps and their immediate vicinity.

The two *Myrmica* species even in the off-stump area show eco-differentiation in their nest distribution. *M. scabrinodis* is especially characteristic of small stumps completely overgrown by the general soil biota and probably therefore unsuitable for *fusca*. It never extends as far into the moister ecosystem-type as does *rubra*, but both overlap in the higher intermediate zones. This type of distribution is well known and has been shown to exist in many parts of Europe.

(*b*) *The distribution on stumps*

The positions of the nests on each of the thirty stumps provided further information about the distribution. These results have been summarized in a diagram (Fig. 1) where the centre of each nest has been indicated in the appropriate position—in the centre of the diagram if the nest covered the whole stump. The results for all stumps have been superimposed, but for clarity each species has been plotted on a separate diagram. It is quite apparent that differences existed: *fusca* tended to occupy southerly

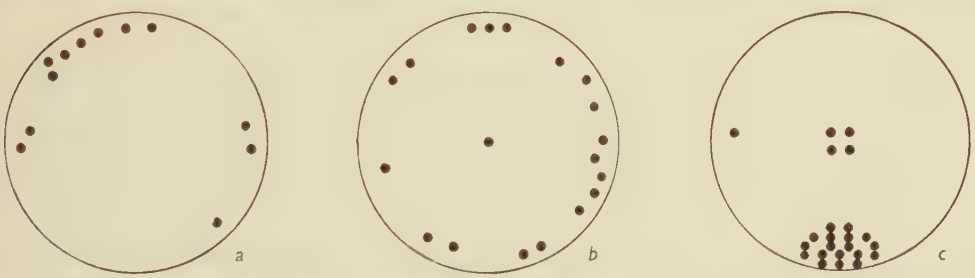

Fig. 1. The positions of the centres of ant nests in thirty stumps, superimposed and reclassified by species: (*a*) *Myrmica rubra*, (*b*) *Myrmica scabrinodis*, (*c*) *Formica fusca*. North is at the top of the diagram.

sites and often extended over the whole stump (the one exception was in the case of a stump with the whole of the south face eroded); *rubra*, which was never found alone, occupied in all but three instances the north and west sectors, whereas *scabrinodis* was widely distributed but with a tendency to easterly concentration. Hence the distribution within stumps is a miniature of that on and off stumps; *rubra* occurs in the cooler moister places and the others in the warmer drier places. One additional point emerges: that *fusca* nests in warmer places than *scabrinodis*. Thus the order of position from warm to cool is: *fusca*, *scabrinodis*, *rubra*.

Leptothorax acervorum fits into the stump population in a different way. It makes galleries in wood so hard that it appears to be unworkable by the other species. These galleries may be entered by holes so small that the larger species are excluded. Whether they nest in this way from preference or necessity is unknown. In other places in the west of Scotland they appear to seek the sun as much as other ants, and will nest in soft wood to do so—for example in the rotting logs of felled and incompletely removed trees. It is unlikely that they could maintain a nest site in soft wood against *fusca* pressure. Hence the weight of evidence supports the hypothesis that necessity rather than choice governs their nest location, but this cannot be regarded as proven. If so, they owe their existence in this ant population to their small size and their ability to work harder wood than the others.

COMPETITION FOR ARTIFICIAL NEST SITES

(*a*) *Thick stone slabs*

Six stone slabs of irregular shape, 3–6 cm. thick, and roughly a quarter of a square metre in area, were placed in the above habitat in early August. Each was arranged in a desirably exposed and well-drained site so as to be as nearly as possible equidistant from nests of the three species, but these requirements were not always perfectly achieved.

Under the first stone a colony of *scabrinodis* appeared 4 days after laying and remained without interference for the remainder of the summer and the following winter. But with the resumption of activity in the spring, *fusca* began invading from a corner away from the main concentration of *scabrinodis* galleries. After 3 weeks, by the end of April, *fusca* occupied the whole stone, and remained as long as observations continued, that is through the two succeeding summers.

The second stone was also occupied by *scabrinodis*, after 4 days. They remained throughout the experiment. The nearest *fusca* nest was 2 m. away.

The third stone was occupied by *rubra* and *fusca* at the same time from different directions and again within 4 days of setting. The *fusca* colony was weak, that is, composed of few and small workers, and the two species remained together throughout the first summer, sometimes making contact and at others separated by unoccupied areas. There was clearly ample room for both under the stone. From early October until early April, whilst the *rubra* colony were away from the surface, the *fusca* made no attempt to occupy their empty galleries. At the end of April the *rubra* left but the cause of this could not be ascertained. It was not until 2–3 weeks later that *fusca* expanded and filled the whole stone site. This they continued to do throughout the remainder of the summer, the following winter, and the next summer as far as the end of August. At this time the *rubra* reappeared under the corner that they had previously inhabited. It seems clear from this that the *fusca* were either too weak to monopolize the site or lacked the necessary stimulus.

Rubra occupied the fourth stone-site for the whole of the first summer, and as is their custom disappeared from the surface about mid-October. At the end of the following March they were seen inspecting the remains of their old galleries but so also were *fusca* workers. *Fusca* alone occupied the site and remained throughout that and the following summer.

Stone number five was well exposed in spring before the birch leaves unfurled, but afterwards was slightly shaded at most times of day. The first summer both *scabrinodis* and *fusca* entered but never in any strength. The next spring *fusca* alone were present, this time in strength, but they thinned out considerably as tree shade developed. *Scabrinodis* re-entered at this time (mid-May) and stayed until August, making distinct galleries which *fusca* never approached. Additional indication of the low summer competition pressure at this site was given by the entry of a *rubra* colony with its own galleries in another part of the stone. In the last summer of observation *fusca* alone were present.

The last of these six sites was first entered by *rubra*; they were soon followed by a *fusca* colony, which surrounded them but did not entirely eliminate them until September. Even so they reappeared in one corner next spring, but by the end of April had been once more driven out, leaving as their only trace a number of dead and dying workers. The *fusca* monopoly lasted this and the following summer when observations ceased.

Thus of six stones four were initially occupied by one or other of the *Myrmica* species and two by *fusca* and a *Myrmica* species. After two and a half summers only one stone remained with *Myrmica* alone (*scabrinodis*), four were with *fusca* alone, and one with both *fusca* and *rubra*. In general then a tendency from *Myrmica* towards *fusca* was shown, verifying the previous speculations from distribution analysis. But the inter-species relationships were not simple and a number of modifying circumstances emerged. *Fusca* pressure was only high and monopoly-tending where strong colonies previously existed near to desirable sites; weak colonies might coexist with either or both species of *Myrmica* in ideal sites, and strong colonies able to monopolize sites in spring with full insolation allowed the *Myrmica* species to enter in summer shade. Monopoly was achieved by direct aggression accompanied by the destruction of opposing workers.

(*b*) *Slates*

This type of investigation was extended, using smaller artificial nest sites, with the object of increasing the intensity of interspecies reaction; these were slates 25 × 15 cm., and 0·5–1·0 cm. thick. To obtain more information about the two *Myrmica* species 15 of these were placed in an area of lightly sheep-grazed acidic grassland devoid of *fusca* (and *acervorum*), and only 10 in the plagioclimax felled-woodland. They were spaced at 14 m. intervals and examined each week for 2 years.

During this time five changes were noticed under the 15 grassland slates, all from *rubra* to *scabrinodis*. The slates were set in late autumn but remained untenanted until spring; by 9 April, 12 were occupied, 7 by *rubra* and 5 by *scabrinodis*. By the end of the summer all sites were occupied, but only 4 by *rubra*, the rest (11) by *scabrinodis*. In the next summer only one change took place, leaving 3 *rubra* and 12 *scabrinodis* nests. Thus four of the five changes were in the first and one in the second summer.

In the other habitat with 10 slates the following changes occurred: one replacement of *rubra* by *scabrinodis*, two replacements of *Myrmica* (one of each species) by *fusca*, and one replacement of *scabrinodis* by *rubra*. In this last case the *rubra* was a strong and the *scabrinodis* a weak colony. Later this *rubra* left and the *scabrinodis* returned, but not into the *rubra* galleries. A week later *fusca* entered this site and rapidly drove

the *scabrinodis* out altogether. The inter-*Myrmica* changes took place in the first summer, but the *fusca-Myrmica* changes in the second.

Thus the 25 slates showed 0, 1 and 2 changes in the ratio 17 : 7 : 1, indicating that in the particular circumstances a considerable measure of stability was the rule. The dominant position of *fusca* was confirmed and further evidence provided that *scabrinodis* is able to replace *rubra* (except when very much weaker).

(*c*) *Turf banks*

Further information about the interaction of the two *Myrmica* species was obtained by studying the colonization of banks made from turfs, (piled two high to give a height of about 20 cm.) arranged in a line running roughly east-west, and backed with soil. Grass on the top and front (with southward exposure) was repeatedly cut to 5–10 cm. to maintain full soil insolation. The bank was 4·5 m. long, and 0·3 m. broad. It was constructed in the autumn of 1947, and by July 1948 there were established in it two *scabrinodis* and three *rubra* colonies (the latter of the form *microgyna*). *Scabrinodis* **A** was a large colony of large dark workers, and was fully mature as it produced sexuals. *Scabrinodis* **B** was a smaller colony of smaller paler workers. *Rubra* **A**, **B** and **C** were all mature colonies.

Frequent daily observation showed that *scabrinodis* **A** workers were besieging all *rubra* nests, and especially that nearest to their own (*rubra* **A**). Parties of workers were stationed day and night outside these nests, and, on the appearance of a *rubra* worker at the entrance, a very characteristic behaviour took place. After a chance contact, both the workers involved withdrew abruptly through about half a centimetre, with antennae adducted, so bringing the tip of the funiculus back into line with the mandibles. After side to side movements of the head the *scabrinodis* worker (never the *rubra*) would suddenly jerk forwards and backwards through about a centimetre. This was repeated until either a leg or an antenna of the *rubra* worker was grasped in the mandibles. If contact was not made after five or six times, the *scabrinodis* usually withdrew and crouched in a soil crevice. By these means, any *rubra* worker that ventured carelessly to the nest opening was seized and dragged outside. Here more *scabrinodis* workers would fasten themselves on to its other appendages and remain so until these were amputated. *Rubra* workers with limbs and antennae missing are a common sight at such times; they do not seem to retaliate. Forel (1921) has recorded similar behaviour and he adds that this species may rob larger ants of their prey, displaying considerable tenacity when molested in the process. Donisthorpe (1927) cites a number of records of *scabrinodis* feeding on *Lasius flavus*, often living in the latter's mound to reduce transport difficulties. It is possible that some of the captured *rubra* workers were eaten but this was not noticed. It is fairly certain, however, that *rubra* males were eaten, for by mid-July they had appeared from pupae in colony **A**, and those that came to the colony entrance were seized by *scabrinodis* workers and taken away.

During July, very few *rubra* workers were seen outside the nests, and these were usually mutilated to varying degrees. Thus one was seen grasping a blade of grass with its mandibles; its left antenna, first and second legs on the left side, second and third legs on the right side, and the tibia and tarsus of the last leg on the right side

were missing. A general exodus of sexuals began on 26 July and many were caught by *scabrinodis*.

On the first day of August the colony *rubra* **A** had vacated their site and left the bank, and a small group of *scabrinodis* workers were near but not inside. The last week of July had been hot and dry, and the top 5 cm. of soil in the *rubra* **A** galleries was dry. The two other *rubra* colonies remained, but **B** was a little further east than previously. *Scabrinodis* workers were in the top soil about 15 cm. away. A slate was put between these places to encourage interaction. A week later (8 August), a new *scabrinodis* brood position had been established about a metre away, much nearer to *rubra* **B** than any hitherto. Surprisingly, it was *rubra* that colonized the slate, and brought in brood gradually. This was done by *rubra* **C**, a colony which had earlier been stained with neutral red (Brian in press) to assist in identification. *Rubra* **B** also moved a little. No further changes took place that year and *rubra* were confined to the east end of the bank. Next spring, 1949, *rubra* **C** failed to reappear, and *scabrinodis* workers were active under the slate moving soil, but they never brought brood there. During April they molested *rubra* **B** especially violently, and this colony evacuated in mid-May during a severe drought.

Thus after less than 2 years the bank, initially populated by three *rubra* and two *scabrinodis* nests, became entirely occupied by the latter species. The large colony actively besieged the *rubra* colonies which left successively, the first to go being the nearest and the last the farthest from the *scabrinodis* nest. In two cases evacuation was during drought and in one during winter. The *scabrinodis* did not extend their nests into the vacated zones.

(*d*) *Other examples of replacement*

A few additional examples of replacement were obtained in the course of other investigations. In May 1949 a *rubra* colony under a stone was replaced by a *scabrinodis*. This occurred during a drought in which the relative humidity of the air in the upper galleries of the nest fell to 60%. At this time also a colony of *rubra* under a slate was replaced by a *scabrinodis*. In June 1949 a *rubra* colony on a stump in a permanent quadrat was replaced by a *scabrinodis*, and a similar change was seen in a bank with sandstone slabs on it; at this time, as before, the ground was unusually dry. All these results were without bias as all replacements observed were recorded. Finally the incident described elsewhere (Brian in press) of a *scabrinodis* colony replacing a *rubra* colony during winter under an observation slate may conveniently be recalled here.

Thus under slates, in banks, and in stumps fifteen replacements have been seen, fourteen from *rubra* to *scabrinodis*, and one the other way. Hence evidence is not lacking from a variety of sources about the existence and direction of replacement in *Myrmica* populations.

THE CAUSE OF REPLACEMENT

The cause of replacement in cases of *fusca* occupation seems in no doubt; it is a gradual aggressive advance of nest site into zones previously occupied by one of the *Myrmica* species. This has been described under stone slabs, and the two examples under slates were similar. The qualifying conditions of nest-site attractiveness and aggressor

strength have been mentioned. But the situation between the *Myrmica* species is different; it was striking how frequently a sudden replacement occurred, a site belonging to one species one time, and the other next time. In fourteen cases of *scabrinodis* replacing *rubra* this happened during drought nine times, during winter twice, and only three times when no clear climatic stricture accompanied the change-over. In these cases, therefore, two extreme theories about the mechanism are possible: (1) that *rubra* go suddenly when the siege pressure of *scabrinodis* becomes unendurable; (2) that *rubra* are more easily dislodged by climatic unfavourability, and *scabrinodis* are quick to occupy the vacated sites.

The evidence for the first of these alternatives is meagre; in the three nests that changed species in the absence of apparent climatic adversity no evidence of siege was available, but other irritants may have been present. The only positive evidence of removal under siege pressure was an intraspecific interaction in which a strong *scabrinodis* colony besieged a weak one occupying a slate; after compression the latter vacated suddenly, but their galleries were not occupied until some hours later (Brian in press). This makes it possible that siege could act interspecifically in this way.

The bulk of evidence favours the second hypothesis. The extent to which removal took place in drought and over-winter has been mentioned. It has been found moreover that *rubra* move more than other species under these conditions, when there is no evidence of interference by other Formicids. Thus in a permanent quadrat in a felled woodland biotic plagioclimax (full details of which will be given elsewhere) after one winter seven *rubra* and two *scabrinodis* nests changed position, while *fusca* nests all returned to the same place. During the drought in June–July 1949 none of 13 *scabrinodis* nests moved, whereas 6 out of 28 *rubra* nests moved into different positions—this in spite of the fact that the former species occupied the drier terrain in the first place. In the experiment with 25 slates already discussed *rubra* often vanished in dry weather, sometimes reappearing with rain, sometimes going altogether. Through the 2-year period no *scabrinodis* nests disappeared without clear biotic cause, and five *rubra* colonies disappeared for 1 or 2 weeks during drought and then reappeared; one failed to return after hibernation, the slate remaining vacant for several months. Instances of this sort under the stone slabs may be recalled and other examples in experiments primarily for other purposes have been noticed but need not be specified.

It has also been found that *scabrinodis* workers visit the surface galleries of their nests in winter whenever the temperature rises above 8° C. A survey of slates, whose summer species composition and distribution was known, was made in mid-November when the surface temperature was 8° C. and there was no sun. Two *fusca*, 11 *rubra* and 11 *scabrinodis* nests were expected; only six sites showed workers at the surface—all *scabrinodis*. With an expected equal frequency of the *Myrmica* species this result has a probability of 1·56% by chance. This survey was repeated at the end of February with an air temperature of 6° C. and sunshine; the same relative frequencies were expected, but this time one *fusca*, one *rubra* and seven *scabrinodis* were observed. The chances of this result, (disregarding *fusca*) are 3·13%. More intensive observations of this type have been recorded elsewhere (Brian in press). Finally to add further support to the climatically induced theory of *rubra* replacement is the experimental

demonstration by Gösswald (1938, 1941) that *scabrinodis* are more tolerant of and resistant to low humidities.

Direct aggression of *scabrinodis* against *rubra* appears rare. Gallery by gallery replacement similar to that used by *fusca* in dealing with the *Myrmica* species seems to occur infrequently, although it has been observed (Brian in press). Siege, although known to occur, does not inevitably follow from proximity of the two species; thus many old ant sites appear without it and myrmecologists consider it worthy of record. It can perhaps be regarded as primarily a predatory reaction and this has in fact been the general interpretation up to the present; in this case, its frequent absence may perhaps be attributed to the presence of an alternative food-supply. Nevertheless the fact that a weak *scabrinodis* colony has been seen to bolt under the pressure of a stronger one (Brian in press) suggests that siege may occasionally contribute to *rubra* emigration, in such cases no doubt reinforcing climatic stimuli.

Thus there exists ample evidence that a mobile tendency responsive to physical environmental stimulation interferes with the permanent establishment of *rubra*, and enables the more tenacious *scabrinodis* to occupy the relatively exposed sites and to retain them through periods of summer drought and winter frost. Such sites are at their best in spring and autumn, when air temperatures alone are often insufficient for brood development; *scabrinodis* takes full advantage of this.

HABITAT SELECTION BY QUEENS

Ants like other social Hymenoptera are capable of considerable discrimination in their choice of nesting site. *Rubra* sexuals in nuptial condition are attracted to areas of terrain with high light-reflecting properties. They will settle on pieces of white paper, and their usual mating region is a path or other area of sparse vegetation. In addition to this a visual orientation object such as a tree or building appears advantageous although not essential. The *rubra* queen after fecundation rises from the nuptial area and flies away in a direction largely determined by wind, but it is probable, although difficult to determine, that she continues to react to light-intense topographical features. The nuptials of *fusca* and *scabrinodis* are too inconspicuous to settle these points.

There is, however, no doubt that fecundated queens of all species tend to congregate on tree stumps, and on these their distribution is far from random. By a fortunate chance an area of about 2000 sq.m. of 15–20-year-old pine plantation adjacent to the heavily populated area repeatedly referred to in this paper, was felled. This was in December, and by the end of the following summer the pre-afforestation stumps, well-rotted and large (0·5–1·0 sq.m. in area) were heavily populated with queens, principally *fusca* and *rubra*. On one stump, which is illustrated in Fig. 2, 23 queens were found: 12 *fusca*, 10 *rubra* and 1 *scabrinodis*. The *fusca* were mostly on the south side, diffused over a considerable area, with each queen in a separate crevice; the 10 *rubra* were in four groups, one of four, one of three, one of two, and one alone, in easterly situations; the single *scabrinodis* was also easterly.* Other stumps, although

* Experimental and statistical observations on queens of this species are much hampered in this area by their scarcity.

less densely populated, showed similar distributions, the ants being concentrated in the south and east sectors, whilst the north to west sector remained empty. In general, *fusca* occupied the best and *rubra* the second best zones.

Fig. 2. The distribution of twenty-three queens on a single freshly colonized stump. Squares, *Formica fusca*; triangles, *Myrmica scabrinodis*; circles, *M. rubra*. In groups lines join the marks. North is at the top of the diagram.

It was then found by laboratory experiment that such distribution could result from active interspecific competition. A circular glass vessel 10 cm. in diameter with coarse soil in the bottom was placed against a water-bath at 30° C., making contact at one point. Room temperature was 17° C. Dealate fecundated queens were added, three at a time, and their positions periodically noted. In five trials of this sort with *fusca* the queens settled every time at the warmest point within 10 min. With *rubra*, on the other hand, although there was a tendency to settle near the warmth, the queens appeared to be more occupied in searching out a satisfactory crevice. Their aggregation was also less intense, and on only two of the five trials were they associated in a single group. When three *rubra* and three *fusca* queens were inserted simultaneously, the *fusca* quickly and invariably occupied the warmest part independently of the *rubra*

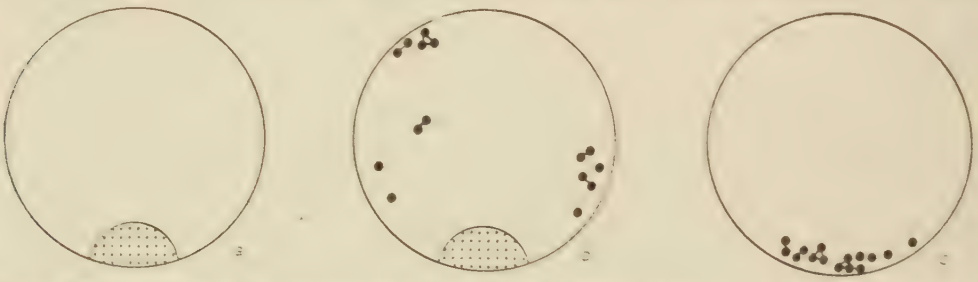

Fig. 3. The settlement of the positions of queens (added in groups of three) in a glass vessel heated to 30° C. at the lowest point. (*a*) *Formica fusca* alone, zone of settlement stippled; (*b*) *F. fusca* and *Myrmica rubra* together; (*c*) *M. rubra* alone. Dots are joined where queens formed groups.

queens. These settled in various places (Fig. 3), always avoiding contact with the *fusca* queens. It is thus clear that the dominance of *fusca* over *rubra* applied to queen interactions as well as to the interactions of colonies. But although this prevents *rubra* from occupying the best sites in a stump at colonization it can rarely drive them into

the north and west, merely into the east.* It is only as a result of subsequent colony growth and perhaps the immigration of *scabrinodis* colonies that this takes place. Normally this is a slow process, for woodland is not usually felled until the pre-planting stumps have been completely dispersed, and the initial colonization of the bared ground and hard tree-stumps depends upon the prior activity of many other organisms. Thus it has been shown (Brian & Brian 1951) in certain cases that ants only began to appear after 2 years, and after 5 years small to medium-sized colonies were present in the Scolytid-mined zone beneath the bark.

DISCUSSION

This study has brought to light some of the causal patterns determining the distribution. The co-existence of the four species depends upon a combination of habitat, ant-heterovalency, and species differences. A speculative review of the present situation would seem permissible.

Formica fusca receives no check in its tendency to occupy the best sites, but is probably limited in the other direction by its inability to build in vegetation mounds that are capable of reaching sunlight. This species will clearly be started in this distribution by the thermotactic properties of the queens, and the fact that many may assemble on a single stump to form a pleometrotic colony will accentuate this tendency. *Leptothorax acervorum* is probably excluded from the best sites by *fusca*, and in the other direction, as with *fusca*, by its architectural incompetence. Apparently it only exists at all in this area by virtue of its ability to bore into harder wood than the others, since this combined with its smaller size prevents them entering its galleries. *Myrmica scabrinodis* is also kept from the best places by *fusca*, but unlike *acervorum* can extend into the vegetated areas and build mounds. But what determines the extent of its penetration into these less favourable areas is as yet unknown: perhaps *rubra*, perhaps its feeding methods, perhaps its temperature requirements. *M. rubra* is kept out of the best nest sites by *fusca* and by *scabrinodis*, the latter indirectly through its greater tenacity of these sites during their occasional temporary unsuitability. In the other direction *rubra* is limited by its inability to breed at the air-shade temperatures prevailing in the west of Scotland in summer (Brian & Brian 1951).

It is hoped to complete this analysis of distribution after further study, especially of the feeding methods and food of the ants. A full account of the differences between the *Myrmica* species is also being prepared.

SUMMARY

1. In an area of felled-woodland subsere, where biotic plagioclimax had become established, ant conditions had probably been favourable for about 20 years. It was shown that the four species present were distributed in different proportions on and off the rotting stumps, and that characteristic species positions on the stumps were also established.

* This will of course depend upon the degree to which *fusca* and *scabrinodis* colonize. There is evidence to suggest that these species produce sexuals less often and in smaller numbers than *rubra*. It is possible too that their range of dissemination is less.

2. By placing artificial sites—stones, slates, or banks of turf—in such a way as to encourage reaction it was established that a species replacement order existed, only reversed in cases of extreme disparity in colony size or periodic unsuitability of the habitat.

3. Replacement was either by direct aggression (in the nest site, or by siege parties from a distance) or by substitution during (otherwise) temporary absence caused by either drought or cold. Different methods were characteristic of different species, but some latitude existed.

4. Even the foundress queens had a species-replacement order, but the degree to which this operated in normal conditions was probably slight.

5. It was concluded that the period of vegetational stability had lasted long enough to enable a development from an initially near-random distribution in the favourable regions—primary loci of colonization—to a species-differentiated distribution over the whole habitable area. This arose in a heterovalent environment through the existence of a replacement order, differences in architectural capacity, and differences in climatic tolerance.

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OBSERVATIONS ON THE DIURNAL BEHAVIOUR OF THE REDTAIL MONKEY (*CERCOPITHECUS ASCANIUS SCHMIDTI* MATSCHIE) IN A SMALL FOREST IN UGANDA

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(With 9 Figures in the Text)

INTRODUCTION

In recent years a considerable amount of information has been published demonstrating the important part played by monkeys in the epidemiology of yellow fever in Uganda forests. Haddow, Smithburn, Mahaffy & Bugher (1947) produced evidence which strongly suggested that yellow fever in Bwamba County, Toro District, Uganda, was primarily an enzootic in monkeys, transmitted from monkey to monkey by an arboreal mosquito which was active after sunset. Haddow, Dick, Lumsden & Smithburn (1952) have recently extended this premise to include all forest areas in southern and western Uganda. *Aëdes* (*Stegomyia*) *africanus* Theo. has been shown to be the principal vector in this cycle (Smithburn, Haddow & Lumsden 1949). It was also suggested by Haddow, Smithburn, Mahaffy & Bugher (1947) that the most likely route for the disease to be passed on to man was by a forest monkey infected with yellow fever raiding the adjacent crops, being bitten by a mosquito biting predominantly at crop level, which in turn passed the infection on to man cultivating in the same place. Lumsden (in press) has shown quantitatively that *A.* (*Stegomyia*) *simpsoni* Theo. was the most likely vector to infect man in the crops, a hypothesis suggested by Haddow, Smithburn, Mahaffy & Bugher (1947). Furthermore, yellow fever virus has been isolated from this species captured in cultivated areas more than once (Mahaffy, Smithburn, Jacobs & Gillett 1942; Haddow, Smithburn, Mahaffy & Bugher 1947).

Haddow, Smithburn, Mahaffy & Bugher (1947) suggested that *Cercopithecus ascanius schmidti* Matschie, the redtail monkey, was the most likely of the several species present to carry the infection into the crops, since it was common in the forest strips and in the main body of the Semliki Forest, and was in the habit of raiding native crops for food.

More recent work by Haddow *et al.* (in press) has shown that the redtail population of Uganda shows the highest standardized immune rate (52·9%) to yellow fever of all the monkey species adequately sampled. They also showed that *C. a. centralis* Neumann, the grivet or grey monkey, which to a large extent is terrestrial by day, showed a standardized immune rate which was significantly lower (35·0%) than that of the exclusively and mainly arboreal species, of which *C. a. schmidti* is one. This difference in immune rates is significant even when samples for the two species from the same area are compared.

It was therefore felt that an investigation of the habits of these two species might

* The author died in Uganda a few days before this paper went to press.

yield results of importance in relation to the epidemiology of yellow fever. Both are abundant on Entebbe Peninsula, though not always abundant in the same place at the same time. It was decided first to study the redtail monkeys in Zika Forest, a small forest situated at the base of the peninsula and readily accessible by road from Entebbe, since it was known that this forest contained a considerable permanent population of this species (shown in the present study to be about thirty-five individuals).

The quantitative data on which this paper is based were collected by African observers manning observation posts in various advantageous positions overlooking or inside Zika Forest. Lumsden (1951), and Buxton (1951) have previously made use of a similar technique to gather quantitative zoological data in the field, and have found that, provided the work was straightforward and only a low standard of writing was required, the Africans were reliable.

DESCRIPTION OF THE AREA

(*a*) *Topography*

Zika Forest is in Busiro County, Mengo District, Uganda, situated seven miles inland from Entebbe Township on the shore of the Entebbe Peninsula, one of many such peninsulas forming the heavily indented northern coastline of Lake Victoria. The forest is on the north-western side of this peninsula, bounding the head of a small swamp-filled bay off the main arm of the lake.

The forest is U-shaped in plan (Fig. 1) with the apical half of the U filled in by forest, and arms extending out from the U along the shore. In cross-section it is saucer-shaped, i.e. the centre of the U forms the flat bottom of the forest, and the arms and perimeter of the U are on the slopes, which are gradual at the apex and steeper along the arms. The flat floor of the forest is perennially waterlogged, whereas the raised area, except for a narrow marginal region between the slope and the flat floor, is well drained.

(*b*) *Botany*

The following botanical description of the area is based on information kindly supplied by Mr H. C. Dawkins, Forest Ecologist of the Forest Department of the Uganda Government. The nomenclature of tree species follows Eggeling (1940).

Zika Forest is part of the formerly more extensive lake-shore forests of Mengo District, and botanically it is typical of many such forests still extant. Ecologically the forest may conveniently be divided into three zones, each with its characteristic vegetation, as follows:

(1) Permanent swamp in which the water-level is always at or above ground-level.

(2) Raised wet forest areas that are never flooded but where the water-table is permanently close to the surface and readily accessible to tree roots.

(3) Raised seasonal forest in which the water-table is such that free water is not perennially available to tree roots.

Over thirty tree species are known to be present in the forest, of which by far the largest number are confined to the raised seasonal forest. The characteristic species for each zone are as follows:

(i) Confined to permanent swamp: *Mitragyna stipulosa* (DC.) O. Ktze., *Erythrina excelsa* Baker, *Voacanga obtusa* K. Schum.

(ii) Species occurring in permanent swamp, but also in raised wet forest: *Macaranga schweinfurthii* Pax, *Spondianthus ugandensis* Hutch., *Uapaca guineensis* Muell. Arg., *Raphia monbuttorum* Drude.

(iii) Species characteristic of raised wet forest which are also found in raised seasonal forest but never occur on flooded sites: *Pseudospondias microcarpa* (A. Rich.) Engl., *Parkia filicoidea* Welw., *Macaranga monandra* Muell. Arg.

(iv) Species confined to raised seasonal forest, and incapable of standing waterlogging: *Lovoa brownii* Sprague, *Maesopsis eminii* Engl., *Piptadenia africana* Hook. f., *Phialodiscus unijugatus* (Bak.) Radlk., *Sapium ellipticum* Pax, *Albizzia grandibractiata* Taub.

The corresponding characteristic plants of the forest floor are:

(i) *Marantochloa purpurea* (Ridl.) M.-R., *Aframomum sanguineum* K. Schum.

(ii) *Marantochloa leucantha* (K. Schum.) M.-R., *Sarcophrynium schweinfurthianum* (Kantze), M.-R.

(iii) *Phrynium confertum* Benth., *Pollia condensata* C.B.Cl., *Butorrestra imperfortata*, C.B.Cl.

(iv) *Leptaspis cochleata* Thwaites, *Streptogyne gerontogaea*, Hook. f.

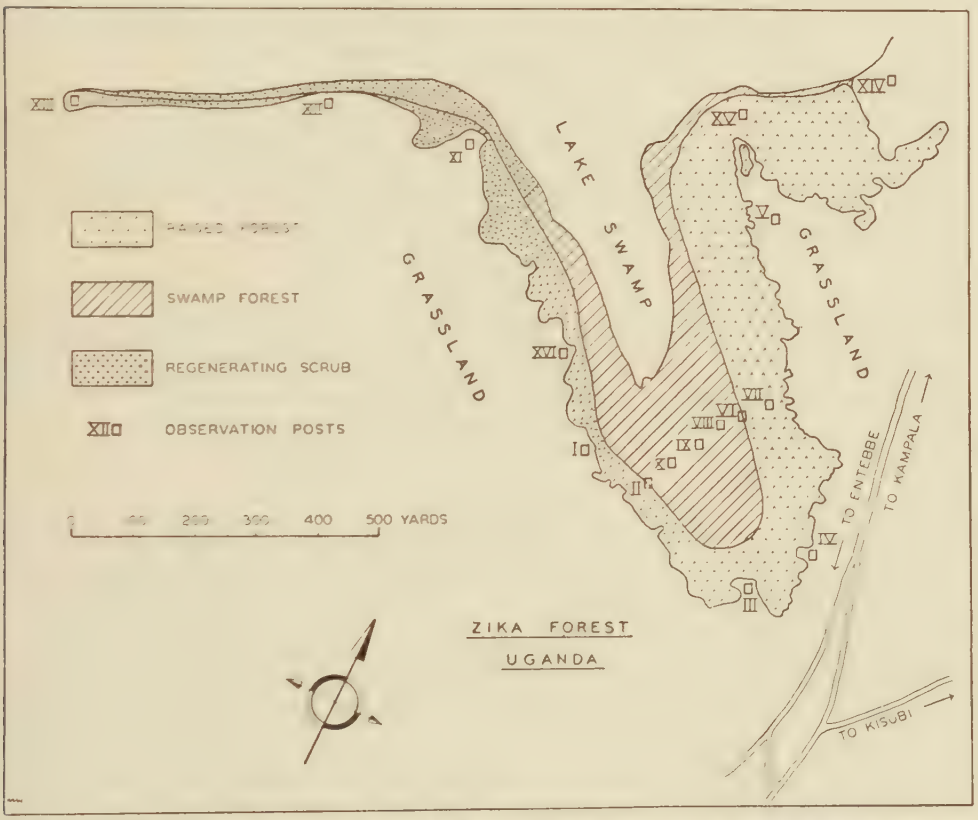

Fig. 1. A sketch-map of Zika Forest, Mengo District, Uganda, showing the positions of the observation posts and the distribution of raised and swamp forest, drawn largely from aerial photographs.

Fig. 1 shows the approximate distribution of the three main forest types in plan. It should, however, be borne in mind that the swamp forest as defined on this map is not homogeneous, but owing to the uneven nature of the forest floor raised wet forest sites occur interspersed throughout the swamp forest, and the characteristic raised wet forest trees grow on these sites. This is shown in Fig. 2, which is a diagrammatic cross-section of the forest cut through the line of observation posts (see below)

running from one side of the forest to the other. Raphia palms are shown on this diagram occurring in raised ground in the swamp forest. These areas should properly be marked as raised wet forest in Figs. 1 and 2, but it was necessary to assume a simplified structure of the forest in order to be able to divide the records of monkeys seen between raised and swamp areas. In interpreting the monkey observations, those seen in the raised seasonal and raised wet forest areas shown in Figs. 1 and 2 have been classified as raised forest observations, and those seen in the mosaic of raised wet forest sites surrounded by swamp forest, included in the areas marked as swamp forest in Figs. 1 and 2, have all been classified as swamp forest observations.

Fig. 2 also shows diagrammatically the distribution of understorey trees, and the nature of the dominant vegetation below the understorey level. In the swamp forest this is made up largely of Marantaceae and Zingiberaceae, the species of which are listed above, but shrubs predominate in the raised seasonal forest and the characteristic herbs are not conspicuous. The importance of the distribution of understorey trees in relation to the visibility from observation posts, and the habits of the redtail will be discussed below.

The relative heights of the canopy in the raised seasonal forest in the neighbourhood of post VII and of the swamp forest is also shown diagrammatically, but it must be emphasized that the vegetation shown is not drawn to scale either with respect to the numbers or the dimensions of the trees present.

(*c*) *Geology*

The forest-grassland boundary at the top of the raised forest follows the division between lateritic ironstone above, and mica schist below. The surface soil in the forest is formed of decayed mica schist and humus. This information was kindly supplied by the Department of Geological Survey of the Uganda Government.

METHOD

The observations on which this paper is based were all made by the African field staff of this Institute. The work was supervised by the writer who visited the observers at various times of the day. All the observers were fully familiar with the appearance of *Cercopithecus ascanius schmidti*, which was the only monkey seen regularly, and of *C. aethiops centralis* which was seen occasionally, and it is most unlikely that the two species were ever mistaken for each other. No other species of monkey occurs in Zika. The majority of the observers were men of the Baamba tribe, who inhabit Bwamba County, Western Uganda, where they had been employed by this Institute on various investigations in forest. During the course of this work their observational powers and knowledge of monkeys was amply proved. Many of them were partially illiterate when the present study was begun, but after a period of teaching and close supervision they were found to record accurately what they saw. The work done in the first week was regarded as training and the results from it are not included below.

The observation posts were chosen to give a good view of different parts of the forest, taking into account the topography and different ecological associations present. These posts were distributed and numbered as shown on the map (Fig. 1). A description of each post is given below.

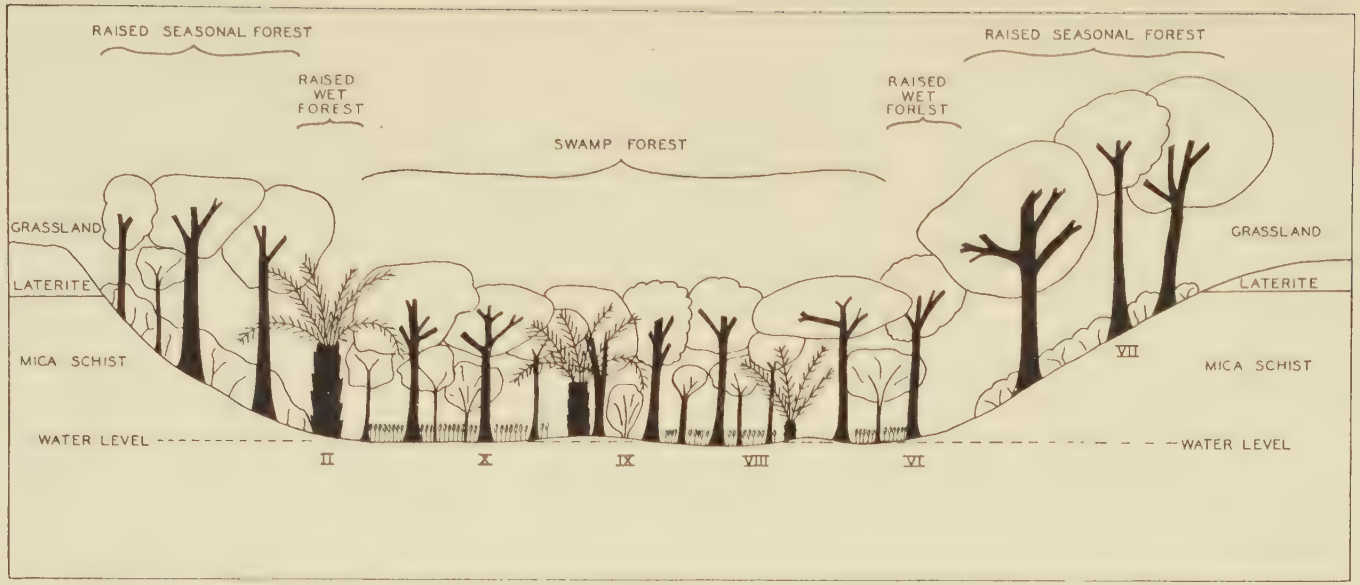

Fig. 2. A diagrammatic cross-section of Zika Forest taken through the line of posts which ran from one side of the forest to the other. The distribution of the raphia palm (*Raphia monbuttorum* Drude), the main vegetational types of the forest floor, Marantaceae and Zingiberaceae in the swamp forest, shrubs in the raised seasonal forest, the relative height of the main canopy and the relative density of the understorey in different parts of the forest are also shown diagrammatically with respect to the distribution of the observation posts. The figure is not drawn to scale.

As far as possible, the observer at each post was changed each day in order to minimize the effect of any differences in efficiency between observers. In any one week the same posts were occupied on each day as far as possible. The number of men available for the work varied, but it was not possible, except during one week, to carry out observations throughout all the hours of daylight on any one day. During the first and second weeks observations were made from mid-day to dusk, and from dawn to mid-day respectively. Observation was carried out during the whole daylight period on 16–18 May from five posts, and on 19 May from four posts. For all subsequent weeks observations were carried out from midday to dusk on Monday, Wednesday and Friday, dawn to midday on Tuesday and Thursday, and dawn to 1100 hr. sun-time on Saturday. In this way it was considered that maximum use was made of the available man-power. To ensure that observation was started before first light and was not stopped before it was dark the writer was always present in the forest when observation was due to start at dawn, and was usually present at last light when evening observations were in progress.

Each observer was equipped with a compass card marked in 10-degree intervals, a clock, a notebook and a pencil. Clocks were standardized at the beginning of each period of work and were set so that sunrise was always within 2 min. of 0600 hr., and sunset within 2 min. of 1805 hr. The 24 hr. clock is used for all times in this paper. The compass card at each post was orientated by the writer, using a magnetic compass so that all cards were placed with their 0–180° axes pointing to the magnetic north and this axis was marked on the ground, usually with two sticks, for future reference. To ensure that the sticks had not been moved the orientation was checked on subsequent visits. Each observer recorded the number of monkeys seen, the species of monkey, the direction in which the monkeys were observed, the time of observation to the nearest 5 min. and the occupation of the monkeys as either sleeping, sitting, moving, travelling or feeding. A monkey was recorded as moving when its movements were apparently random and did not take it out of the confines of one or two trees; play was included in this category. When young were seen they were usually recorded separately.

It is not claimed that the observations are a completely true record of what was seen nor that the observers saw all the monkeys in their area, but it is considered that any errors of omission in them are unbiased and will not have any serious effect on the conclusions reached. Errors of exaggeration may also have occurred, but the effect of these is probably unimportant owing to the numerous observations, the consistency between different observers, and the fact that the writer saw nothing during numerous visits to lead him to doubt the accuracy of the records.

Rough notes on the weather were kept each day by the senior African observer present. The general state of the weather was recorded hourly as well as the time of beginning and end of rain. For the last 18 days of observation the temperature registered by a black bulb thermometer, exposed horizontally 2 ft. above ground-level in full sunlight, was also recorded every quarter of an hour.

Each 5 min. period of observation from each post has been treated below as one unit observation period. Each monkey seen per unit observation period is treated as one monkey-observation. To find out the diurnal activity rhythm the monkey-

observations made in each 5 min. period between 0525 and 1830 hr. from all posts on all days were summed. Because the number of observation periods which made up this total was not the same for each 5 min. period, owing to differences in the number of observers available at different times, the total numbers of monkey-observations were adjusted to a standard number of observation periods for each 5 min. period. To obtain a relatively smooth graph from these standardized figures the moving mean of three standards was calculated for each 5 min. interval of time and this moving mean plotted. The value plotted for each 5 min. interval was therefore the mean of the standardized totals of monkey-observations for that period and the periods immediately preceding and following it. It will be shown below that the sum of the monkey-observations at any one time is a good indication of the state of activity of the population at that time.

The observations have also been used after similar treatment to produce information on: (*a*) the relative importance of different types of forest, (*b*) the effect of weather on activity, (*c*) feeding times and feeding trees, (*d*) troop size, (*e*) proportion of young to adults, (*f*) the constancy with which one part of the forest is used, and (*g*) the population of redtails in the forest. The statistical terms and methods used are taken from Simpson & Roe (1939).

OBSERVATION POSTS

The sixteen observation posts were selected for a number of different reasons. Visibility varied markedly in the different types of forest, being least in the swamp, and greatest in some parts of the raised forest in which there were only forest canopy trees and low bushes, the understorey probably having been cut for firewood. The number of days on which each post was occupied is shown below:

17–21 April	I, II, III, IV, VI
24–28 April	I, II, III, IV, V
10–13 May	I, II, III, IV, V
16–19 May	I, II, III, IV, V
1–2 June	II, VI, VII, VIII, IX
5–10 June	II, III, VI, VII, VIII, IX, X
12–17 June	I, V, XI, XII, XIII, XIV
19–24 June	II, III, VI, VII, VIII, IX, X
17–22 July	I, III, V, X, XIV, XV, XVI.

The total time of occupation of each post is given in Table 7.

The position of each post (see Figs. 1 and 2) and the time when it was to be occupied were not determined before the work started. It was only after the first 3 weeks of observation that it was realized that the swamp forest and the extremities of the forest might be of particular importance. As the behaviour of the redtail varied in different areas a brief description of each post is necessary.

Post I was at the top of a steep slope well above the level of the swamp forest. In the foreground there was an area of regenerating scrub where raised forest had been cut down. A considerable area of swamp forest was visible directly in front of and below the post as well as some raised forest on either side. The post was on the edge of the forest with the observer's back to open grassland.

Post II was at the end of a path leading down to a waterhole more or less at the

boundary of the raised wet forest and the swamp forest. The area under observation was approximately half raised forest, and half swamp forest.

Post III was near the apex of the forest in an open clearing containing some banana plants and coffee bushes with a good view of raised wet forest, and of a little raised seasonal forest.

Post IV was in a position very similar to that of post I, overlooking a cleared area opening on to swamp forest, and flanked by raised forest with the observer's back to open grassland.

Post V was in grassland in the centre of the bend that occurs as the forest follows the shore of the lake eastwards from the main forest area. From this post there was a good view on three sides of the raised forest margin and of trees at the top of the slope. On the fourth side several patches of scrub and trees were visible growing round old termite mounds rising out of the lateritic ironstone in an otherwise open grassy area.

Post VI was at the end of a wide path leading down to a waterhole in a similar position to that of post II. It was completely surrounded by forest, one half of which was raised and the other swamp forest.

Post VII was about 70 yards up the slope from Post VI, where it was completely surrounded by tall forest canopy trees of the raised seasonal forest. Visibility was very good in nearly all directions as there was very little understorey growth in this area.

Posts VIII–X were all on a path cut through the swamp forest between posts II and VI. In order to improve the visibility, a certain amount of clearing had to be done round each post. Post IX was put on a platform 15 ft. above ground-level for this same reason, and posts VIII and X were put on low platforms in order to give the observer somewhere to sit above water-level.

The line of posts from II to VII (Figs. 1 and 2) cut right across the forest, so that any monkeys moving on this line were likely to have been seen while these posts were occupied.

Posts XI–XIII were in positions chosen to give good visibility over the forest strip following the shore westwards from the main part of the forest. This strip had been largely cleared of trees, and consisted of regenerating scrub, much of which was made up of seedlings of *Raphia monbuttorum* (Raphia palm). There were a few patches of forest trees still standing. Post XI was on the slope looking on to the regenerating scrub strip, and had a good view of one patch of tall trees. Post XII was in a clearing amongst the regenerating scrub and approximately at water-level. Post XIII was at the end of this lake-shore strip, where the forest stops abruptly and is replaced by thick grass.

Post XIV was at the end of the eastern arm of the forest in the open, facing the end of the raised forest. The observer had his back to banana plantations, a strip of raised forest was on his left and the open lake swamp on his right. There were some patches of trees and scrub between the post and the forest.

Post XV was at the head of the bend in the forest in which post V was situated, but inside the forest and on the boundary between the raised and swamp forest.

Post XVI was placed between posts I and XI and on the opposite side of a patch of raised forest to post I. There was a good view of the base of the western arm of the forest.

RESULTS

(*a*) *Diurnal activity rhythm*

Fig. 3*A* is plotted from all the observations made during the whole period over which the work was carried out. The total number of monkey-observations for each 5 min. period was standardized to represent one hundred observation periods, and the graph is plotted from the moving mean of three such standards.

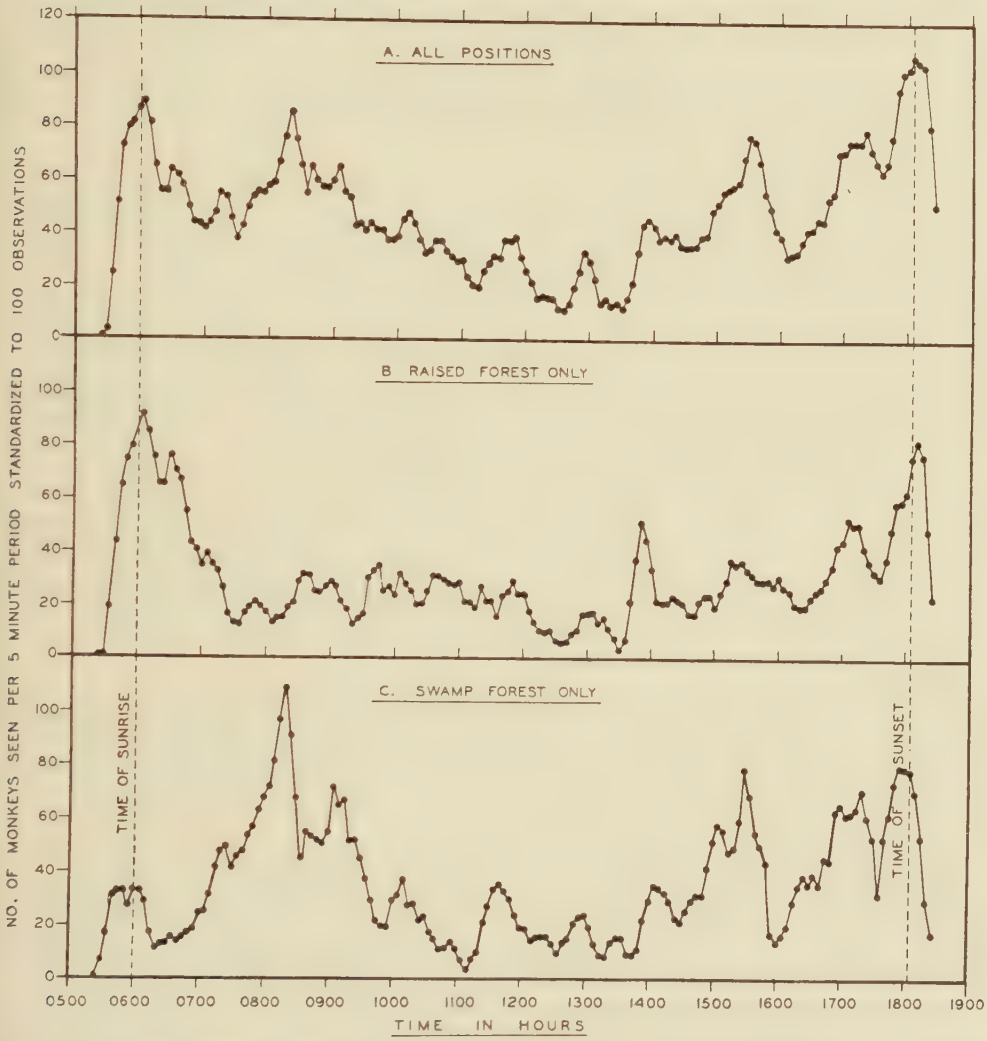
A. ALL POSITIONS
B RAISED FOREST ONLY
C. SWAMP FOREST ONLY
NO. OF MONKEYS SEEN PER 5 MINUTE PERIOD STANDARDIZED TO 100 OBSERVATIONS
TIME OF SUNRISE
TIME OF SUNSET
0500 0600 0700 0800 0900 1000 1100 1200 1300 1400 1500 1600 1700 1800 1900
TIME IN HOURS

Fig. 3. The diurnal activity rhythm of the redtail monkey; curve *A* was derived from all observations from all posts; *B* from all observations made in raised forest only; and *C* from all observations made in swamp forest only. Table 1 shows the original figures summed quarter-hourly on which these curves are based. The time of sunrise and sunset is also shown (broken lines).

It is clear from Fig. 3*A* that activity was by no means uniform throughout the day. There was a marked burst of activity at sunrise, followed by a quieter period till about 0800 hr. when there was another period of great activity, followed by a steady decrease till the early part of the afternoon. At about 1400 hr. activity increased again

and reached another sharp peak at 1530 hr., it fell again till 1600 hr. after which there was a moderately steep rise to a final peak at sunset, and followed by a rapid cessation of movement. It is interesting that the two highest points on the graph occur within 5 min. of sunrise and sunset respectively.

When those observations derived from the raised forest and those from the swamp forest are separated, treated mathematically in the manner described above, and the results plotted, two very different curves are produced (Fig. 3*B*, *C*). Of the four main activity peaks shown in curve *A* it is found that the dawn peak consists almost entirely of observations made in the raised forest, and the peaks at 0820 and 1530 hr. of those made in the swamp forest. The peak at sunset, although occurring in both swamp and raised forest, is a quarter of an hour later in the latter. There is little activity in either area during the middle of the day.

The very sharp peaks of activity shown in Fig. 3 suggest that the activity rhythm for all the individuals in the forest is very closely similar. There was, however, a certain amount of latitude. Posts I and III were about 350 yards apart and overlooked botanically similar types of forest. They were each occupied by an observer on a large number of days (see p. 31). On several occasions monkeys were reported as sleeping within sight of these two posts on the same night so that it may safely be assumed that different groups habitually slept in the neighbourhood of each post. The early morning peak of activity occurred at 0550 hr. for post III, and at 0635 hr. for post I. The meteorological conditions at the two posts were presumably basically the same, though the normal sleeping trees visible from post I are rather more exposed than those of post III. It appears, therefore, that these different times of the early morning activity peak represent definite differences in habit between different groups of monkeys. The peak for post I is made up of observations of monkeys almost exclusively in raised forest, and is therefore comparable with the peak for post III from which only raised forest was visible.

Table 1 gives a summary of the figures on which the three graphs in Fig. 3 are based. The number of monkey-observations and the actual number of observation periods during which observation was made are given per quarter-hourly period. The grouping into quarter-hourly periods was necessary in order to reduce the table to reasonable dimensions.

It will be noticed in this table that the total observation periods shown for all posts is less than the total of swamp plus raised forest observations. This is because posts I, II, IV, VI and XVI overlooked both swamp and raised forest. Monkey-observations from these posts were divided according to the compass card reading into the two forest categories, but the total number of observation periods for each post has been included in the table in both swamp and raised forest columns. Posts XI–XV were not considered to overlook true raised or swamp forest, and have not been included in the calculations of either Fig. 3*B* or *C*.

From the records made by the observers of the occupations of the monkeys it is possible to find out whether the proportion of monkeys sitting still varies at different times of the day. Fig. 4 shows the percentage of redtails seen that were sitting still for all monkey observations for each hourly period of the day. It is apparent from the curve that the percentage of monkeys seen sitting during the part of the day when

Table 1. *The total monkey-observations* (M.O.) *made and the total number of 5 min. observation periods* (O.P.) *during which observation was carried out are given per quarter-hourly period for the sum of all posts, all observations made in raised forest only, all observations made in swamp forest only and for 3 days on which heavy rain fell during the first half of the morning and for which observations are available for the whole day. The times shown are the mid-points of the quarter-hourly periods*

	All		Raised		Swamp		Wet mornings	
Sun time	M.O.	O.P.	M.O.	O.P.	M.O.	O.P.	M.O.	O.P.
0525	0	36	0	33	0	18	—	—
0540	127	207	89	167	37	107	14	39
0555	295	363	214	268	53	196	12	42
0610	308	383	229	270	61	204	9	42
0625	214	384	177	270	26	204	5	42
0640	219	384	179	270	29	204	3	42
0655	164	383	117	269	38	204	5	42
0710	180	381	95	267	65	204	0	42
0725	172	381	44	267	100	204	3	42
0740	189	381	45	267	97	204	0	42
0755	208	381	52	267	128	204	13	42
0810	252	381	39	267	166	204	11	42
0825	281	378	54	264	183	201	18	42
0840	242	378	82	264	111	201	16	42
0855	214	378	70	264	102	201	4	42
0910	209	378	56	264	130	201	4	42
0925	162	369	37	257	102	198	5	42
0940	152	369	85	255	57	198	4	42
0955	137	369	67	255	38	198	2	42
1010	176	369	70	255	73	198	14	42
1025	119	369	52	255	42	198	33	42
1040	135	369	79	255	28	198	55	42
1055	109	366	71	255	26	195	29	42
1110	67	333	51	239	4	170	11	42
1125	83	295	48	222	33	162	24	42
1140	109	293	52	221	57	163	7	42
1155	102	342	59	247	43	190	14	42
1210	72	461	43	330	36	258	18	42
1225	49	314	23	222	26	182	18	42
1240	42	303	13	211	24	179	18	42
1255	99	305	35	222	41	180	17	42
1310	43	309	28	226	23	182	12	42
1325	43	323	18	230	26	193	15	42
1340	71	336	50	234	17	204	6	42
1355	151	336	104	234	45	205	9	42
1410	130	340	50	237	71	209	14	42
1425	127	361	55	248	50	223	31	42
1440	131	373	41	249	67	230	44	42
1455	183	381	60	252	98	234	26	42
1510	220	390	75	258	130	234	2	42
1525	271	397	96	265	141	237	4	42
1540	271	407	81	275	133	245	12	42
1555	169	411	76	279	41	249	26	42
1610	132	412	71	279	49	249	29	42
1625	169	417	57	285	97	252	31	42
1640	185	417	76	285	88	252	16	42
1655	295	418	122	286	157	252	32	42
1710	314	420	145	288	156	252	66	42
1725	301	420	107	288	154	252	29	42
1740	281	420	109	288	133	252	20	42
1755	412	407	164	275	192	242	23	42
1810	408	388	214	260	162	231	28	42
1825	54	105	27	117	9	54	1	1

they are relatively inactive (i.e. from about 1000 to 1400 hr. (Fig. 3)), is not consistently higher than the percentage for the parts of the day when they are active. These results imply that a redtail that is in an active state may be visible whether it happens to be sitting still at the moment or not, but that one that is inactive rests in such a position that it is not easy to see. It seems probable therefore that redtails rest by day in the denser and more opaque tree-canopies in which they are hidden amongst foliage.

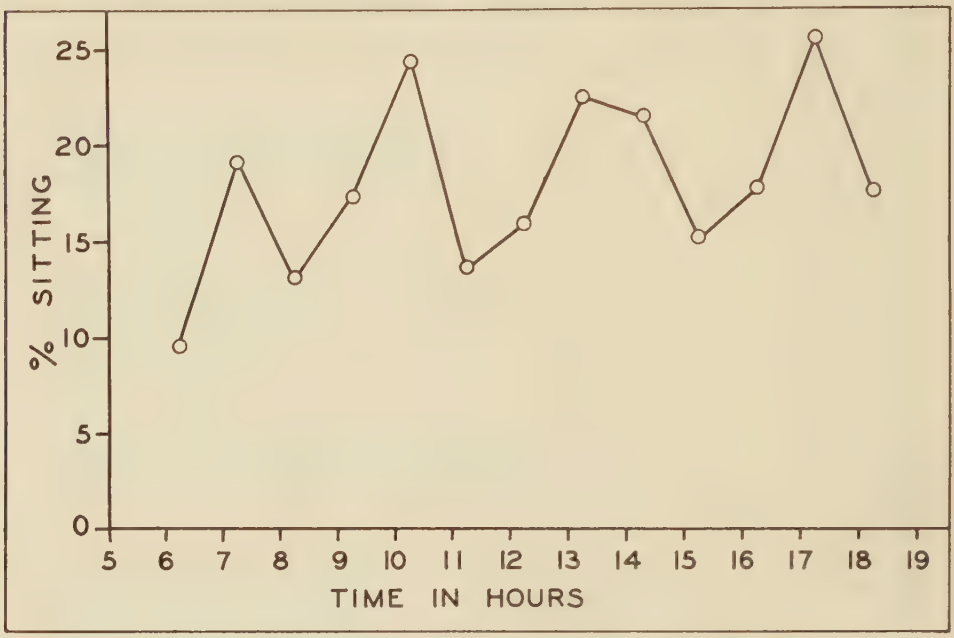

Fig. 4. The percentage of the total monkeys seen in each hour that were sitting.

(*b*) *The effect of weather on activity*

It has not been found possible to draw any conclusion from the weather notes made while observations were in progress, except that heavy rain and high sun temperatures inhibit activity. 16, 18 and 19 May were days on which observations were carried out continuously from dawn to dusk, and also days on which heavy rain fell before 1000 hr. Posts I–IV were occupied on each day, post V only for the first 2 days. The monkey-observations made on these days have been summed, and the moving mean of three sums plotted for each point on the graph (Fig. 5). Each point is based on only forty-two original observation periods so there may be a sampling error, but it is probably not important. The figures on which this graph is based are presented in Table 1 grouped in quarter-hourly periods.

It is clear from Fig. 5 that the major part of the early morning activity peak was postponed until the rain had stopped, the first peak occurring at 1035 hr. The peak shown at 1440 hr. is made up almost entirely of observations of redtails in the swamp forest. The dusk activity peak for these 3 days is early, at 1700 hr. instead of 1800 hr., perhaps because 2 of the 3 days on which these observations were made were particularly cold. The effect of rain on the vigilance of an observer must also be considered, but the writer was present for much of the rainy periods and saw no monkey movement.

It was thought that the period of low activity occurring in the middle of the day as shown in Fig. 3 might be due to some definite meteorological factor, of which solar radiation seemed the most likely. To test this hypothesis a black bulb thermometer was exposed at Zika Forest 2 ft. above ground-level in open sunlight and read every quarter of an hour while monkey-observation was in progress. These readings are only available for the last 18 days of observation. An exposed black bulb thermometer

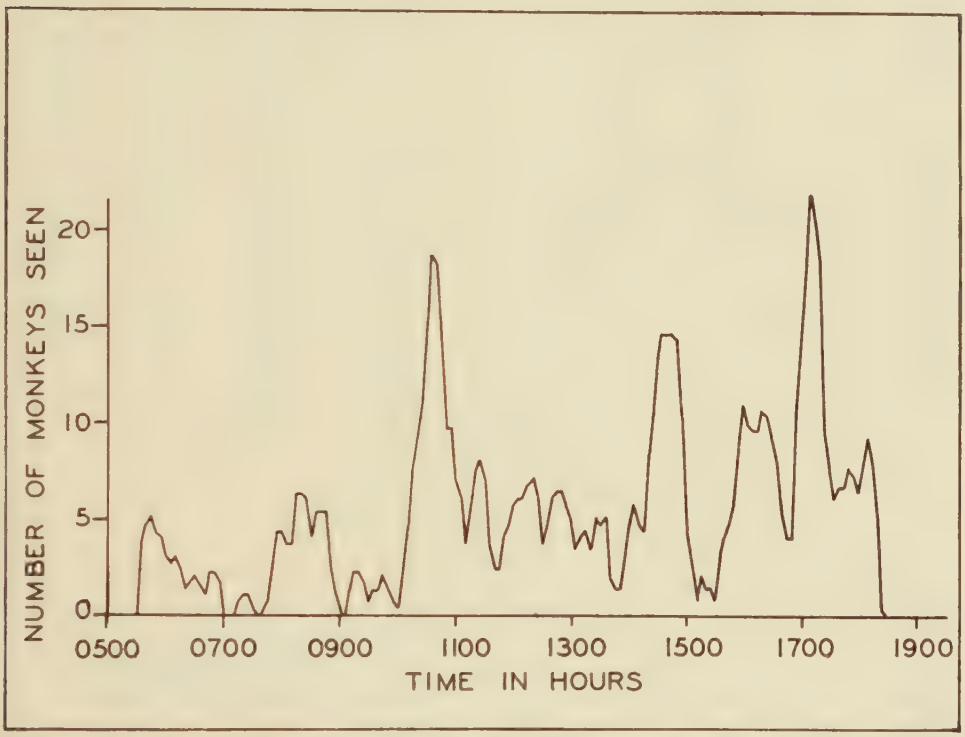

Fig. 5. The activity rhythm shown by the redtail monkey on 16, 18 and 19 May, days on which heavy rain fell before 1000 hr. and for which observations are available from dawn till dusk. The graph is plotted from the moving mean of three of the total monkey-observations for each 5 min. period.

records the equilibrium temperature resulting from the combined effects of wind, solar radiation, radiation from the ground and radiation from the black bulb itself. The latter factor is peculiar to the individual thermometer. The numerical values of the readings do not therefore have any defined physical meaning, but do indicate the order of the resultant effect of the external factors on an inert body. The mean temperature recorded by these observations for each quarter of an hour is shown in Table 2 and Fig. 6, which, when compared with Fig. 3*A*, show that the period of least monkey activity is in fact coincident with the hottest time of day.

The number of monkeys seen per observation period for each ° C. sun temperature between 0855 and 1435 hr. is shown in Table 3 and Fig. 7, from which it is clear that the activity of the redtails decreased markedly at temperatures of over 30° C., but did not alter appreciably at lower temperatures. As the thermometer was only read at every quarter-hour the numbers of monkey-observations and observation periods

given in Table 3 are the totals for the three 5-min. observation periods immediately before, immediately after and at the quarter-hours.

Table 2. *The mean temperature recorded by an exposed black-bulb thermometer per quarter-hour, and the number of observations on which each mean is based*

Time	No. of observations	Mean temp. (° C.)	Time	No. of observations	Mean temp. (° C.)	Time	No. of observations	Mean temp. (° C.)
0545	2	16·0	1000	9	26·9	1415	8	25·6
0600	7	16·4	1015	9	27·2	1430	8	25·6
0615	8	15·9	1030	9	27·1	1445	8	25·4
0630	8	16·4	1045	9	27·8	1500	8	24·7
0645	8	16·8	1100	9	28·8	1515	9	25·1
0700	8	17·5	1115	7	28·7	1530	9	25·3
0715	8	18·5	1130	5	30·0	1545	9	25·3
0730	8	19·1	1145	5	30·4	1600	9	25·1
0745	8	20·3	1200	6	32·5	1615	9	23·5
0800	8	20·9	1215	10	29·4	1630	9	23·5
0815	8	21·9	1230	8	28·9	1645	9	20·8
0830	9	22·7	1245	8	27·5	1700	9	22·2
0845	9	23·9	1300	8	28·0	1715	9	22·1
0900	9	24·7	1315	8	28·4	1730	9	22·4
0915	9	26·2	1330	8	25·9	1745	9	20·4
0930	9	26·2	1345	8	25·7	1800	9	19·7
0945	9	26·3	1400	8	25·6	1815	9	18·9

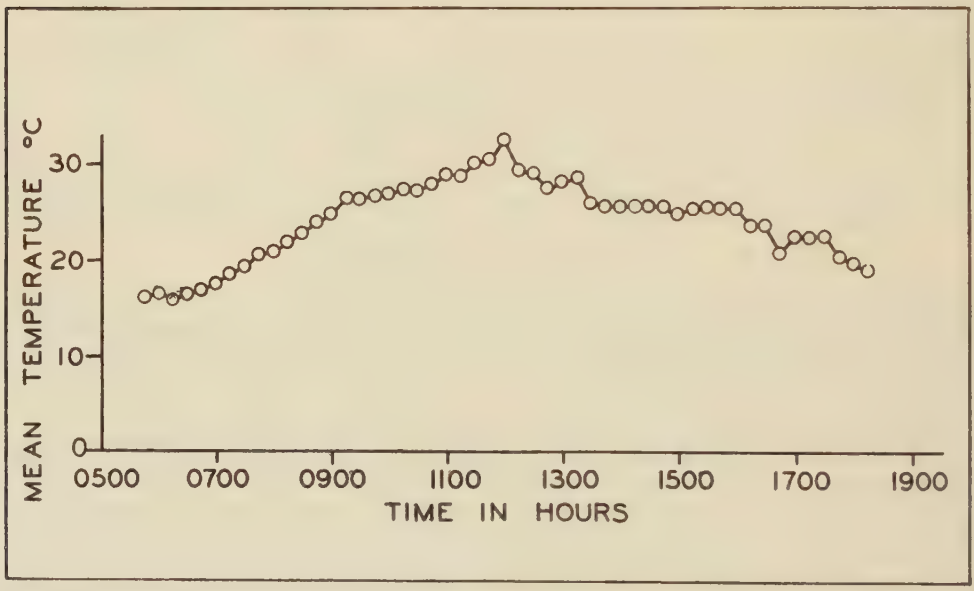

Fig. 6. The mean temperature registered every quarter-hour by a black-bulb thermometer supported 2 ft. above ground-level in open sunlight. The mean is derived from readings taken during the last 18 days of monkey-observation in Zika Forest (see Table 2).

(*c*) *Feeding*

The total number of monkeys seen feeding in each quarter-hourly period is shown in Table 4. Fig. 8 shows the percentage of monkeys seen that were feeding plotted by half-hourly periods, the data being derived from Tables 1 and 4, and the moving mean of three 15 min. totals of monkeys seen feeding, standardized to 300 observation periods. Both curves show that there is a marked outburst of feeding

at sunrise, and a high proportion of the monkeys seen at that time were feeding. Feeding then apparently continues throughout the morning, but at the time when large numbers of redtails were active in the swamp forest at about 0800 hr. (Fig. 3*C*) the proportion seen feeding is low. Between 1030 and 1200 hr. Fig. 8 shows a high percentage feeding, but the general level of activity at this time was low, indicating that of the few monkeys active at this time a considerable number were feeding.

Table 3. *The relationship between the number of monkeys seen and the temperature for each degree centigrade registered by a black-bulb thermometer exposed in full sunlight at Zika Forest for the period* 0855 *to* 1435 *hr., on the last* 18 *days on which observations were made*

Temp. (° C.)	No. of observation periods	Total monkey-observations	Monkeys seen per observation period	Temp. (° C.)	No. of observation periods	Total monkey-observations	Monkeys seen per observation period
19	6	2	0·33	29	68	70	1·03
20	41	51	1·24	30	75	72	0·96
21	41	35	0·85	31	90	69	0·77
22	89	99	1·11	32	77	55	0·71
23	100	84	0·84	33	39	22	0·56
24	113	131	1·18	34	62	6	0·10
25	68	54	0·79	35	49	5	0·10
26	100	86	0·86	36	21	0	0
27	78	71	0·91	37	13	0	0
28	74	84	1·13				

Fig. 7. The number of monkey-observations made per observation period are shown for each ° C. registered by the exposed black-bulb thermometer between 0855 and 1435 hr. (see Table 3).

From about 1200 to 1530 hr. very few monkeys were seen feeding, and it appears that there is a definite break in feeding at this time. Feeding starts again shortly before 1400 hr. and continues to a considerable extent till a short time after sunset. Fig. 8 shows that this feeding period starts rather before the main afternoon activity peak shown in Fig. 3, and that a high proportion of the monkeys seen at this time were feeding. From about 1430 hr. onwards the percentage seen feeding remains fairly low, but the actual number of feeding monkeys shows a rise to a peak at sunset, indicating that the high level of activity of this time of day (see Fig. 3), is not primarily connected with feeding, but that nevertheless a considerable amount of feeding takes place at this time. Haddow (in press) reached substantially the same conclusions from his

examinations of the stomach contents of numerous shot redtails, and showed that the evening meal is on the average considerably larger than the morning meal.

When the observations on feeding monkeys are divided into those from raised and from swamp forest it is found that the raised forest is apparently much more used as a source of food. During both morning and evening feeding times the number of

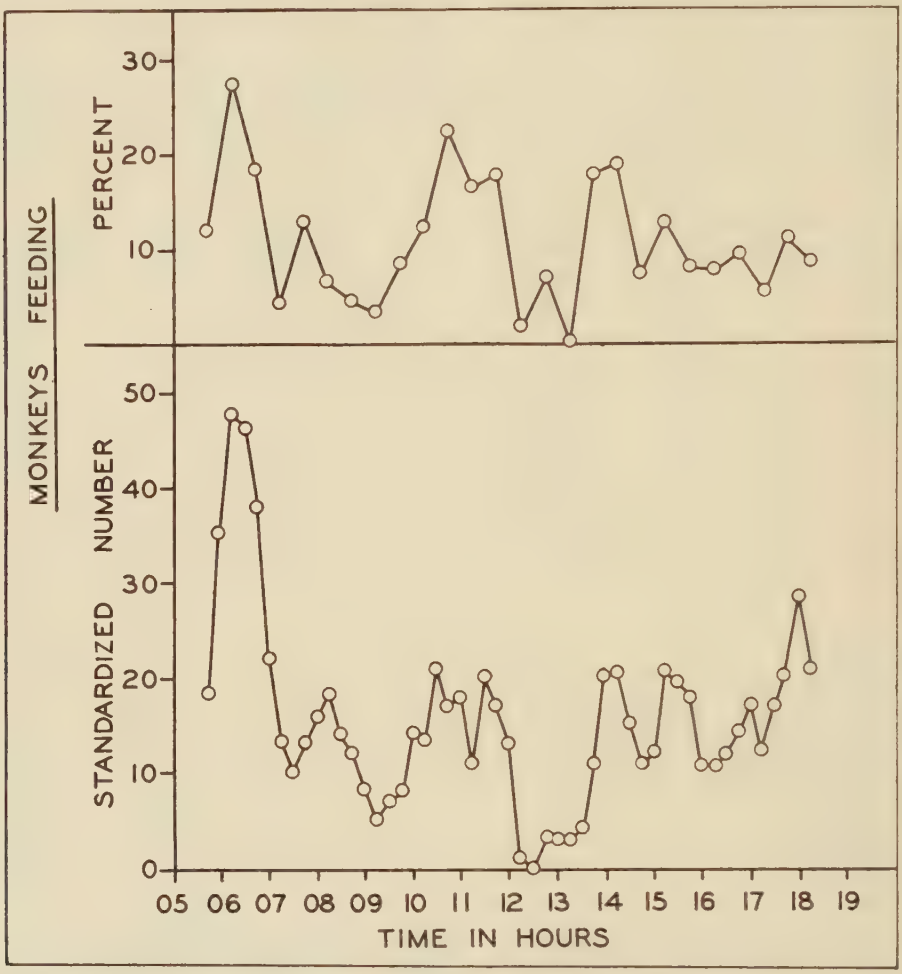

Fig. 8. The feeding rhythm of the redtail monkey. Upper curve shows the percentage of redtails seen that were feeding per half-hour. Lower curve shows the total redtails seen feeding in each quarter-hour, standardized to 300 observation periods and plotted as the moving mean of three such standards. The data on which these two curves are based are given in Tables 1 and 4.

monkeys seen feeding in the raised forest is considerably higher than the number seen feeding in the swamp forest except for short periods, particularly at about 0800 hr. when the swamp forest observations are more numerous, but the percentage feeding at this time is low. The difference, when total feeding observations in the two habitats are compared is clearly significant. The data are as follows:

Total observations of monkeys feeding in the swamp forest	249
Total observations of monkeys feeding in the raised forest	766
Total monkey-observations for swamp forest	3995
Total monkey-observations for raised forest	4153

Whether the raised forest is in fact more used as a source of food will be discussed below.

Table 4. *The total number of redtail monkeys seen feeding per quarter-hour period from all posts, the times given being the mid-points of the quarter-hour periods*

Time	Monkeys seen feeding	Time	Monkeys seen feeding	Time	Monkeys seen feeding
0525	0	0955	12	1425	17
0540	15	1010	28	1440	3
0555	38	1025	8	1455	20
0610	67	1040	42	1510	23
0625	76	1055	12	1525	39
0640	35	1110	10	1540	15
0655	34	1125	15	1555	20
0710	17	1140	36	1610	9
0725	0	1155	1	1625	14
0740	20	1210	2	1640	25
0755	31	1225	0	1655	20
0810	12	1240	0	1710	28
0825	25	1255	10	1725	3
0840	17	1310	0	1740	39
0855	5	1325	0	1755	38
0910	7	1340	15	1810	34
0925	6	1355	24	1825	5
0940	12	1410	31		

In addition to recording the times at which feeding occurred, the observers were asked to show the writer the actual tree that was being fed upon. Botanical specimens were then collected and identifications made by Mr H. C. Dawkins. The following species of tree were recorded as sources of food, unless otherwise stated the fruits were the part eaten; the type of forest in which each tree habitually grows is shown by a number in the right-hand column. These numbers refer to the forest types described on p. 26.

Pseudospondias microcarpa (A. Rich.) Engl.	(iii)
Voacanga obtusa K. Schum.	(i)
Erythrophleum guineense G. Don.	(iv)
Antidesma venosum Tul.	(iv)
Sapium ellipticum Pax	(iv)
Tylostemon ugandensis Stapf.	(ii)
Piptadenia africana Hook. f. (Leaves only)	(iv)
Bosqueia phoberos Baill.	(iv)
Ficus exasperata Vahl	(iv)
F. urceolaris Welw. ex Hiern	(iv)
Raphia monbuttorum Drude	(ii)
Pittosporum ? abyssinicum Del.	(iv)

It is most unlikely that any of these records are erroneous, but it is not always easy from inside the forest to identify the actual tree in which monkeys have been seen feeding by an observer placed some distance away. Many of the trees bore epiphytes or lianas and it was impossible to be sure on all occasions that the tree itself was the source of food, and not some other plant supported by it. Of the above records the only ones that are open to doubt are *Antidesma*, *Tylostemon*, *Bosqueia* and *Pittosporum*. Haddow (in press) gives a more extensive list of the species fed on by the redtail.

(*d*) *Group-size and constitution*

The variation of group-size at different times of day is a phenomenon to which attention has been drawn by Zuckerman (1932) and Lumsden (1951) discussing the formation of sleeping groups.

After trying a large number of different groupings it was found convenient to classify the different sizes of groups arbitrarily into: solitary monkeys; 'small troops' of two, three and four individuals; 'large troops' of five to ten; and 'bands' of over ten monkeys. Groups of these sizes were chosen because clearer results were obtained with them than with any other grouping tried, though all groupings indicated the same general trends. Fig. 9 and Table 5 show the percentages of redtails per group-size per hour of the total number seen in that hour. Each point represents the monkey-observations made from half an hour before the hour to half an hour after it.

Table 5. *The total number of monkeys seen solitary, in small troops of* 2, 3 *and* 4 *individuals, large troops of* 5, 6, 7, 8, 9 *and* 10 *individuals, and in bands of more than* 10 *individuals for each hourly period, and the same number expressed as a percentage of the overall total seen in that hour. The percentage in each troop-size for all observations is also shown*

Period	Total monkey-observations	Solitary		Small troops		Large troops		Bands	
		No.	%	No.	%	No.	%	No.	%
0535–0630	939	91	9·7	504	53·7	304	32·4	40	4·3
0635–0730	716	105	14·7	385	53·8	226	31·6	0	0
0735–0830	917	93	10·1	466	50·8	302	32·9	56	6·1
0835–0930	832	91	10·9	366	44·0	251	30·2	124	14·9
0935–1030	584	45	7·7	300	51·4	194	33·2	45	7·7
1035–1130	389	30	7·7	205	52·7	142	36·5	12	3·1
1135–1230	339	25	7·4	163	48·1	139	41·0	12	3·5
1235–1330	233	19	8·2	103	44·2	99	42·5	12	5·2
1335–1430	490	50	10·2	165	33·7	215	43·9	60	12·2
1435–1530	799	72	9·0	341	42·7	260	32·5	126	15·8
1535–1630	753	81	10·8	391	51·9	176	23·4	105	13·9
1635–1730	1062	100	9·4	591	55·6	356	33·5	15	1·4
1735–1830	1156	110	9·5	597	51·6	397	34·3	52	4·5
Grand totals	9209	912	9·9	4577	49·7	3061	33·2	659	7·2

The hourly figures for each different group-size on which these percentages are based have been tested by χ^2 test to see if the differences between times are significant for the whole day. The results are as follows, there being 12 degrees of freedom in each case, the values of P being taken from a table given in Croxton & Cowden (1939):

	χ^2	P
Solitary monkeys	30	$< 0{\cdot}01 > 0{\cdot}001$
Small troops	110	$< 0{\cdot}001$
Large troops	89	$< 0{\cdot}001$
Bands	380	$< 0{\cdot}001$

The variations in the proportion of each of these group-sizes throughout the day are therefore significant, but it is interesting to note that the order of significance

shown by the solitary monkeys is much lower than that for any other group. The fluctuation in percentage shown by the solitary monkeys may not be caused by a

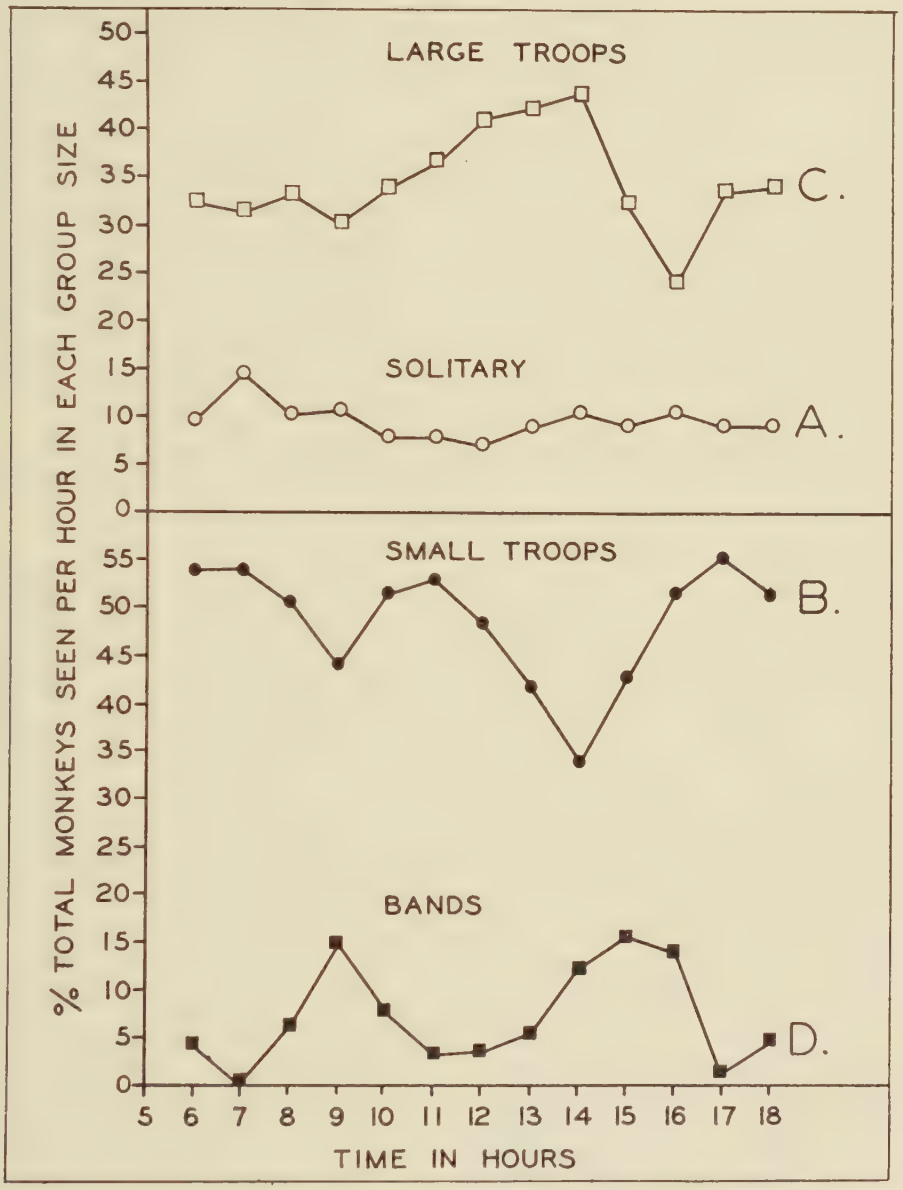

Fig. 9. Diurnal changes in proportion of different troop-sizes. Each point represents the percentage of redtails seen in a particular troop-size for the period from half an hour before the hour to half an hour after it, of the total redtails seen in that period (see Table 5). The troop-sizes have been grouped for convenience into solitary monkeys, curve *A* (open circles); small troops of 2, 3 and 4 monkeys, curve *B* (solid circles); large troops of 5, 6, 7, 8, 9 and 10 monkeys, curve *C* (open squares); and bands of more than 10 monkeys, curve *D* (solid squares).

tendency for more redtails to leave groups, or join them at different times of day, but may be a function of the activity rhythm shown by a steady population of solitary monkeys. This point will be further discussed below.

Fig. 9 and Table 5 also show that for all hours of the day, except one, more redtails were associated in small troops than in any other size of group. The curves for small troops and bands shown in Fig. 9 are approximately mirror images of each other. Large troops exist to a considerable extent at all times of day, but are evidently formed also as an intermediate stage in the formation of bands. The latter occur principally at about 0900 hr., and between 1400 and 1600 hr. These fluctuations in the social constitution of the population at different times of day show that there are periods when small social units tend to aggregate to form larger ones, and other times when the large units split up into smaller ones. These facts are of importance in relation to the study of the function of social aggregations. The percentages of each size of group for the first and last hours of the day are closely similar, and the differences are not statistically significant. It appears therefore that troop-sizes do not change during the night, which agrees with the conclusions of Lumsden (1951). For all monkey-observations made the proportions of monkeys seen in different sizes of groups were: solitary, 9·9%; small troops, 49·7%; large troops, 33·2%; and bands, 7·2%.

Of the 659 monkey-observations of redtails in bands, 375 were made from post X. Why the area round this particular post should have been favoured by the largest social aggregations when other swamp forest posts were not favoured is not known. The largest band seen contained 25 individuals.

The mean group-size for the whole population calculated from the original data was 3·0 monkeys. The total observations of single monkeys was 912; if this number is excluded from the calculation, on the grounds that a single monkey is for some reason not part of the normal social life of the population, then the mean size of groups becomes 3·8 monkeys. It was not possible to calculate the standard errors of these two means as the distribution of the group-sizes did not approximate to normality (see Table 5).

Observers were encouraged to record the number of young monkeys in each group; not all observers did so, but it was felt that any undue persuasion might lead to false records. The records were made in the usual way with a marginal entry to show how many of the group were young, i.e. the number of apparent adults in the group was the total for the group minus the number of young. In calculating the proportion of young from these observations each group has only been counted once; therefore a group that was in view for a quarter of an hour would have been recorded by the observer in three 5 min. periods, but in this calculation has only been included once. It must also be realized that some small groups may have contained no young. These should properly be included in the calculation of the proportion of young, but as there is no means of separating these records from those in which the observation was for some reason imperfect they have been ignored. Another, and very important factor entering into these observations was the distance at which the monkeys were observed, since young monkeys might either be unnoticed, or not sufficiently distinct at long ranges to be recorded. The true number of apparent adults per young is therefore greater than that shown below.

Table 6 shows the frequency of occasions on which young were recorded for each group-size, and the number of young. From these figures the mean number of young per adult may be calculated as follows:

Total number of monkeys observed in groups with young	871
Total number of young observed	282
Therefore total number of adults observed	589
Therefore mean number of adults per young	589/282 = 2·09

The writer formed the impression that most redtail groups in Zika contained young monkeys. It will be seen in Table 6 that on a few occasions more young than adults are reported in a group. It is unlikely that this is ever the true state of affairs, but probably one or more adults actually belonging to the group were not observed. The size of groups of redtails seen in one part of Zika Forest at the same time on different days showed no constancy from day to day, so that it was not possible to trace the movements of individual groups as was done by Lumsden (1951) with *Colobus abyssinicus iturícus* Matschie.

Table 6. *The number of occasions (f.) on which young were reported in troops of different sizes, and the number of young seen in each troop size*

Troop size	No. of young	*f.*	Troop size	No. of young	*f.*	Troop size	No. of young	*f.*
2	1	11	6	2	21	12	3	1
3	1	28	6	3	5	15	4	1
3	2	3	7	2	10	15	6	1
4	1	22	7	3	2	17	6	1
4	2	10	8	2	5	20	4	1
5	1	7	9	2	1	20	6	1
5	2	11	9	3	1	22	6	3
5	3	2	10	3	1	25	7	1
6	1	1	12	2	2			

(*e*) *Population*

No definite estimate of the population of the redtail monkey in Zika Forest can be made from these observations, as it is not distributed at random through the forest. Observation posts vary markedly concerning the number of monkeys seen from them, and one post may vary considerably over a period of time.

The largest number of redtails reported for any 5 min. period from one post was twenty-six. If the observations from all posts for one 5 min. observation period are summed, and the largest of these sums is taken, a figure which is probably close to the total population is found. Observations made from different posts but in such directions that the same monkeys might have been recorded from two or more posts were excluded. The largest figure arrived at by this method is thirty-one. It seems likely from these two observations, and from the general impression gained by the writer during the course of the work in Zika Forest that the redtail population there is more than thirty individuals and less than forty. Dr A. J. Haddow (personal communication) recollects seeing a band of forty-two redtails in Zika Forest in July 1947. The area of the main part of Zika, excluding the long western arm of scrub, is approximately 230,000 sq.yd. The area of forest per redtail, assuming a population of thirty-five individuals, is therefore 6500 square yards, or approximately 1·3 acres per monkey. It must be remembered, however, that monkeys live in a three-dimensional environment and not in an approximately two-dimensional one like a terrestrial mammal.

(*f*) *Distribution of the redtail in Zika Forest*

The distribution of the redtail in Zika Forest was not random during the present work. The number of monkey-observations made per hour of observation, referred to below as the 'observation-rate', is a useful figure for comparing either one post with another, or different periods with each other.

Table 7. *The total number of hours of observation correct to two places of decimals, the total monkey-observations made, and the observation-rate for each post, together with the order of observation-rate of the posts. The mean observation-rate for all posts is also shown together with the total hours of observation and the total monkey-observations*

Post	Hours of observation	Monkey-observations	Observation-rate	Order of observation-rate
I	192·30	1736	9·0	4
II	199·84	1270	6·4	7
III	203·58	1426	7·0	6
IV	116·67	621	5·3	8
V	148·42	477	3·2	10
VI	110·33	140	1·3	13
VII	81·42	40	0·5	15
VIII	80·33	222	2·8	11
IX	78·67	372	4·7	9
X	106·58	1457	13·7	2
XI	28·17	388	13·8	1
XII	34·33	65	1·9	12
XIII	33·84	3	0·1	16
XIV	69·84	516	7·4	5
XV	37·92	45	1·2	14
XVI	37·17	431	11·6	3
Grand total	1559·41	9209	5·9	

Table 7 shows the observation-rate for each post for all observations made at that post, and the data from which it was derived. The overall observation-rate for all posts and all periods of observation was 5·9. Post XI is shown as having the highest observation-rate, but in view of the small number of hours of observation and the fact that nearly two-thirds of the monkey-observations made from that post occurred in one evening, no significance is attached to this result. Statistical comparison between posts is not possible, as the number of monkeys seen from each post will, to some extent, be related to the area or volume of forest visible from that post, which will depend partly on the botany of the area and partly on the contour of the ground. The following conclusions can be drawn from the data:

Posts XI–XIII are spaced out along the western arm of the forest in that order, post XI being nearest the main part of the forest (see Fig. 1). As is shown in Table 7, the observation-rate for each post decreases markedly the farther the post is from the main body of the forest. The conditions of visibility did not differ sufficiently between posts to account for these differences, which can be explained most easily by the hypothesis that the redtails seen in this forest strip are not normally resident there, but make excursions into it from the main part of the forest.

Post XIV, at the end of the eastern extremity of the forest, had the third highest observation-rate for all posts, but no redtails were seen from it before 0715 hr. in the

morning, and only nine after 1700 hr., the latest at 1740 hr., in the evening. These facts suggest that this extremity also was only occupied by an itinerant redtail population, in spite of the fact that the forest composing it was tall, uncut and apparently similar botanically to the forest visible from some other posts.

The observation-rates for posts V and VII were low, that of the latter being the lowest for all posts in the main part of the forest. The view from these posts, but particularly that from post VII, was of tall trees at the top of the raised forest. The tree canopy, except along the forest margins was for the most part of the order of 100 ft. high and was mostly composed of relatively open-crowned trees; there was little understorey growth (see Fig. 2). In comparison, the other posts with a view of the main body of the forest were in areas where the canopy was rather lower and denser, and where understorey growth was considerable. The impression was formed by the writer from personal observation that redtails tend to keep to the middle level of the forest when moving about, are not often seen in the canopy except when feeding and are very seldom seen in high, open canopy. If this is in fact true, then the area at the top of the raised forest on the north-eastern side of Zika is less favoured by the redtail because of its relative lack of thick understorey growth, and because of its high open canopy. It may be mentioned that the redtail is adept at moving through very thick and tangled foliage.

Table 8. *Posts II, X, IX, VIII, VI and VII were occupied for the weeks* 5–10 *June, and* 19–24 *June. This table shows the number of hours of observation, number of monkey-observations and the observation-rate for each post in each week, for each post for the two weeks combined, and for all these posts for the two weeks separately and together*

	5–10 June			19–24 June			Both weeks		
Post	Hours of observation	Total monkey-observations	Observation rate	Hours of observation	Total monkey-observations	Observation rate	Hours of observation	Total monkey-observations	Observation rate
II	35·75	187	5·2	37·17	191	5·1	72·92	378	5·2
X	33·75	613	18·2	36·17	238	6·6	69·92	851	12·2
IX	34·83	245	7·0	30·42	59	1·9	65·25	304	4·7
VIII	35·58	125	3·5	36·67	77	2·1	72·25	202	2·8
VI	36·17	45	1·2	37·00	42	1·1	73·17	87	1·2
VII	36·42	41	1·1	37·42	0	0	73·84	41	0·6
Total	212·50	1256	5·9	214·85	607	2·8	427·35	1863	4·4

Posts VII, VI, VIII, IX, X and II are on a line which runs roughly straight from one side of the forest to the other (see Figs. 1 and 2). As will be seen from the descriptions of the individual posts given above and from an examination of Fig. 2, they vary considerably in the type of forest which is visible from each. It is thought that when all these posts were occupied at the same time no monkeys would have been able to cross the line formed by them without being seen. A comparison of the two weeks during which this line was manned shows that the amount of movement across it varied considerably (Table 8). It is therefore probable that the redtail population of the central area of the forest was different in each week.

Table 8 shows that for the period concerned the observation-rate at post X was more than twice that for any other post, in spite of the fact that there appears to be

little botanical difference between post X and posts IX and VIII. If the posts are arranged in order of their observation-rate in each week the order is close to the south-west to north-east topographical order. Starting with the post with the highest observation-rate this order is X, IX, II, VIII, VI, VII for the first week, and X, II, IX, VIII, VI, VII for the second week and for the weeks combined.

Variations in the observation-rate between successive days at the same post also show that the redtail population inhabiting one area of forest is not at all constant from day to day. Post III was occupied for a greater number of hours than any other post (Table 7), and has therefore been selected to illustrate these differences between days. When the days on which less than five hours observation were carried out at this post are excluded, twenty-nine are left for comparison. As will be seen from Table 9, the observation-rate for these twenty-nine days varies between 21·3 and 0·0. Similar variations between days occur in the observation-rates for the other posts. As has been stated the weather on different days has some effect on activity, but an examination of the weather records showed that there was no relationship between high and low activity and different types of weather for post III.

Table 9. *Showing the number of hours of observation before and after noon, number of monkey-observations made and the observation-rate for the days on which post III was occupied for more than 5 hr. The time is expressed in hours correct to two decimal places*

A.M.				P.M.			
Date	Hours of observation	Monkey-observations	Observation-rate	Date	Hours of observation	Monkey-observations	Observation-rate
24 Apr.	6·58	28	4·3	18 Apr.	5·92	14	2·4
25 Apr.	6·83	33	4·8	19 Apr.	6·17	9	1·5
26 Apr.	6·83	82	12·0	20 Apr.	6·25	35	5·6
27 Apr.	6·92	99	14·3	21 Apr.	6·00	25	4·2
28 Apr.	6·75	40	5·9				
16 May	6·33	19	3·0	16 May	6·25	27	4·3
17 May	6·33	33	5·2	17 May	6·25	32	5·1
18 May	6·33	23	3·6	18 May	6·25	133	21·3
19 May	6·25	0	0	19 May	6·25	13	2·1
6 June	7·00	30	4·3				
8 June	7·00	82	11·7				
10 June	5·58	17	3·0				
20 June	6·67	65	9·7	19 June	6·25	60	9·6
22 June	6·50	70	10·8	21 June	6·42	60	9·3
18 July	6·58	37	5·6	19 July	6·33	48	7·6
20 July	6·67	52	7·8	21 July	6·00	9	1·5
22 July	5·75	86	15·0				
Total	110·90	796	7·2	Total	73·34	465	6·3

(*g*) *Night-resting habits*

Considerable previous information is available on the night-resting habits of the redtail (Haddow, Smithburn, Mahaffy & Bugher 1947; Lumsden 1951). From the observations recorded during the present work in Zika Forest, it is not possible to state which individual trees there were used as sleeping trees by the redtail. Each observer recorded the directions in which monkeys were seen to within 10°, but no record of the distance of the monkeys away from the post was made. It is therefore

only possible from the records to state that redtails were seen inactive before dawn, and after sunset in constant directions from the same post on different days. The writer was, however, present at one or other of the posts at dawn and dusk on most of the days of observation, so that more detailed conclusions may be drawn from the numerical data than would otherwise be possible.

Sleeping groups were reported from the following posts during the present work: I–V, VIII–XI and XVI, but those reported from positions VIII–XI and XVI showed no evidence of using the same trees, or the same areas of forest on different nights.

The majority of the redtails seen to be stationary from post I before sunrise and after sunset were observed in the directions 350, 000 and 010°. Most of the days on which these observations were made were days on which feeding was observed in the late evening or early in the morning in the same directions. Observations made at similar times from post II show definite preferences for certain areas but also a wide variety of different directions were occupied on different nights. From post III redtails were most usually seen inactive at dawn and dusk in the area between directions 260 and 340°. On several occasions the writer has seen six or eight monkeys settling down or waking up in this area, not in a confined group but scattered about in singles and pairs in different trees. Similar observations were made from post IV between directions 290 and 320°. It was noted from all posts, but from this post particularly, that the redtail often does not sleep high up in trees, but in thick lower foliage either in the lower branches of large trees, or in the top branches of small understorey trees. Two sleeping areas were recorded on more than one occasion from post V.

The majority of these sleeping areas were in the raised forest. The activity curves in Figs. 3*B* and *C* also indicate that the majority of redtails sleep in the raised forest, the evening peak of activity in Fig. 3*B* being a quarter of an hour later than that in Fig. 3*C*, suggesting that the redtails moved out of the swamp forest into the raised forest at this time. The virtual absence of activity at sunrise in the swamp forest shown in Fig. 3*C* supports this conclusion very strongly.

Lumsden (1951) observed that the redtail usually sleeps among small twigs. This finding is confirmed. He also found that the redtail was often still moving when it was almost too dark to see it in the evening, and that it started moving in the morning before it was light enough for accurate observation, which is supported by the graph of the percentage of monkeys seen that were sitting still (Fig. 4).

Lumsden (1951) gives the mean size and standard error of sleeping groups, excluding solitary monkeys, for each of the four commonest species of monkey in Mongiro Forest, that for the redtail being $4{\cdot}81 \pm 0{\cdot}22$ for eighty-one groups. The corresponding figure for the redtail in Zika Forest cannot be precisely calculated as few observations were made of monkeys actually sleeping. If, however, the mean and standard error are calculated for all individuals seen in groups before 0600 hr. and after 1800 hr., the distribution of group-sizes being approximately normal, the result is $3{\cdot}64 \pm 0{\cdot}14$ for 183 groups. When these two means and standard errors are compared it is found that they are significantly different, the ratio of the difference between the two means to the standard error of the difference between the two means being 4·6.

(*h*) *Social behaviour*

Zuckerman (1932) describes in detail the social behaviour of a colony of hamadryas baboons (*Comopithecus hamadryas* (Linn.)) kept in captivity, as well as that of a party of wild chacma baboons (*Papio comatus* E. Geoffroy) which he observed in South Africa. He shows that behaviour within and between family parties is based on an inter-male dominance scale, and the fact that an adult female undergoes a continuous series of menstrual cycles unbroken by periods of anoestrus. The dominant male in a party exercises a continuous and close control over his females and maintains his position by fighting. A family party may include one or more 'bachelor' males, but they will have no sexual relationship with the females, though they may have homosexual contacts with other males. Copulation and sexual activity were frequently observed in daylight between members of the captive colony, and considerable sexual activity was observed amongst baboons in the wild.

The detailed observation of monkeys in a forest is not easy as foliage obscures much, but the writer has devoted a considerable amount of time to watching the redtail monkey through prismatic binoculars. At no time has any direct sexual activity been seen nor has fighting or threatening amongst adults ever been seen or heard. Several of the African observers used in this work had considerable previous experience of observing monkeys in the wild and none of them claim to have seen any monkeys copulate, except the anubis baboon, *Papio doguera tessellatus* Elliot.

The group of baboons observed in the wild by Zuckerman were in the habit of travelling in a body unless disturbed, in which case they moved off in one direction, but in a widely scattered formation. The redtails observed at Zika often travelled from one place to another in a fairly compact party, but on several occasions, particularly when leaving a feeding tree, they moved off singly with several minutes between the first and last individual. On one occasion a party of ten was disturbed while in a large tree and moved off gradually. The largest individual present sat on an exposed branch and 'barked' at the observer every 2 sec. or so for 6 min. after the last of the rest of the band had left. When this individual moved off it went in the direction directly opposite to the rest of the party and was observed to continue alone until out of sight. Similar observations have been made at other times.

Zuckerman also states that grooming by one baboon of another frequently occurs in nature. The writer observed grooming on only two occasions by the redtail monkey, once in the morning activity period between two individuals, both from their size believed to be females, and once in the evening by individuals of unknown sex.

Fitzsimmons, quoted by Zuckerman, states that *Cercopithecus aethiops pygerythrus* (F. Cuvier) in South Africa is in the habit of posting sentinels when feeding. Zuckerman saw no sign of such behaviour in the chacma baboon nor did the writer in the redtail monkey. On occasion, however, while a party of monkeys was feeding in a tree, one or more might start feeding after the others, or feed in a desultory manner. When not feeding such a monkey was often conspicuously placed, and facing outwards from the feeding tree. Stories that monkey troops have leaders are widespread in the anecdotal literature, but have little reliable backing. The writer saw no sign whatever

of leadership, either vocal or by the behaviour of one monkey in relation to its fellows. When redtails were alarmed they usually moved off in one direction in a fairly compact bunch, but the movement gave no appearance of being in any sense organized.

(*i*) *General observations*

Haddow *et al.* (in press) discussing the role which monkeys play in the epidemiology of yellow fever in Uganda divided the species up into the following groups by habit: (1) exclusively arboreal, (2) mainly arboreal and (3) to a large extent terrestrial. They put the redtail into the second group, a view which is confirmed by the present work. Redtails, though normally seen in trees, were reported on the ground at Zika Forest on a few occasions, both inside the forest and on grassland outside it, they were also seen once or twice in isolated clumps of trees which were not accessible by arboreal routes. They were reported as feeding on the fallen fruits of *Raphia monbuttorum* in the swamp forest.

Except during three weekly periods, 17–21 April, 12–17 June and 17–22 July, the redtail was the only species of monkey seen in Zika Forest, or in the surrounding area. During the first week of observation grivet monkeys (*Cercopithecus aethiops centralis*) were seen in the area and were reported from post II. Between 12 and 17 June grivet monkeys were reported from post XIV on two days, and between 17 and 22 July they were seen from posts I, V, XIV and XVI on several occasions. A few observations were made of redtails concurrently with grivet monkeys from the same post, but no observations on the reactions of one species on another are available.

No evidence was produced during the course of the work to suggest that the redtail population of Zika Forest was subject to fluctuations due to emigration or immigration. Observers in the peripheral observation posts never saw redtails leave the immediate vicinity of the forest, nor did the African owners of surrounding banana plantations, which were not for the most part very close to the forest, complain of raiding by this species of monkey.

DISCUSSION

As explained above, it is considered that any errors made by the observers in the present work will have had an unbiased effect on the conclusions drawn. Some observers were undoubtedly better than others, but the observations made by them were probably better in quantity rather than quality. For instance, early in the work some of the observers wrote so slowly that they probably missed seeing some monkeys while recording others.

It must also be considered whether the standard of observational efficiency is likely to have varied appreciably at different times of day, particularly in view of the conclusions regarding the activity-rhythm of the redtail and the relationship between number of monkeys seen and increasing solar radiation (Table 3 and Fig. 7). For the following reasons the writer is satisfied that any variation in efficiency is not of importance to the conclusions drawn. First, the peaks of activity shown are very sharp and clearly defined, which would not be the case if the reduced period of activity shown following a peak was in fact due to the waning of enthusiasm among the observers after a given period of observation. Secondly, if the long period of relative inactivity

shown in the middle of the day in Fig. 3*A* was due to an increasing lethargy among the human observers, partly because of a rise in temperature and partly because of fatigue, then it would be expected that a sharp rise in monkey activity would be shown shortly after midday, as at this time the observers were fresh, having just started work for the afternoon period. Thirdly, Lumsden (1951) shows a curve for the activity-rhythm of two captive redtail monkeys derived from personal observations on two successive days which is similar to that of Fig. 3*A* in the present paper.

It is thought that the process of summing the monkey-observations for a given 5 min. period of sun time is a valid method of arriving at the activity-rhythm. It is well known that a moving animal is considerably easier to see than one that is still, particularly if it is cryptically coloured. The redtail monkey in its natural habitat is very hard indeed to see unless it is moving, facing the observer, or its tail is hanging in the open, a view which is supported by Allen, Lawrence & Loveridge (1936). The face is conspicuous because of the white heart-shaped area covering the nose, and the area of thick long white hair extending up the side of each cheek. The tail, which is a medium russet-red for its distal half to two-thirds, is sometimes allowed to dangle below a tuft of leaves in which the body of the monkey is wholly concealed, in which case the position of the monkey is obvious. The general colour of the dorsal surface and limbs of the redtail when seen at a distance is dark grey-brown with a tinge of yellow, whereas the ventral surface is pale cream. A redtail in an active state may sit but will never remain still for long. Allee, Emerson, Park, Park & Schmidt (1949) point out that a state of activity at one time of day logically argues a state of relative inactivity at another time and that the inactive period will be spent in a more or less protected environment. The only physical factors known to inhibit redtail activity by day are heavy rain (Fig. 5), and high sun temperatures (Fig. 7). The only predator likely to attack it is the uncommon monkey-eating eagle, *Stephanoaetus coronatus* (Linn.) (Haddow in press). The situation giving maximum protection from these three adverse factors is afforded by the thick, heavy foliage forming the crowns of many of the trees at Zika and from observation it is almost certain that these trees are used as shelter during the diurnal inactivity period. A redtail resting by day is therefore likely to be invisible owing to its choice of resting place, as the thicker canopies are quite opaque when seen from below. It is therefore thought that the graphs shown in Figs. 3 and 5 represent the activity-rhythm of the redtail accurately for the period of daylight in the conditions appropriate to each graph.

As stated above, the number of observations made of monkeys feeding in the raised forest was greater at all times of day except one than the number of those feeding in the swamp forest. It is, however, not possible to show that one type of forest was more important as a source of food than the other for the following reasons. First, visibility in different parts of the forest will affect the proportion of monkeys in a given area that are seen. Secondly, in parts of the forest where there are many species of trees but few individuals of each species, such as the raised forest, there will be a tendency for the monkeys to concentrate for feeding in the few trees that are available at any one time; whereas in those parts where there are many individual trees of each species, but few species, there will be a tendency for the monkeys to disperse when feeding on a particular tree species. The records suggest that some such arrangement

does occur. For instance one individual *Sapium ellipticum* in the raised forest visible from post I was used as a source of food on all days during the first and second weeks of observation. There were also 29 other raised forest trees which were conspicuous and in which large numbers of redtails were seen feeding on several days, notably two individual *Pseudospondias microcarpa*. Monkeys feeding in these few raised forest trees provided a large part of the bulk of the total feeding observations. No single tree was observed to be fed on to any extent in the swamp forest at any time, though several observations were made of redtails feeding on the fruits of different individuals of *Raphia monbuttorum* and *Voacanga obtusa*. *Mitragyna stipulosa*, the dominant tree in the swamp forest, has never been recorded as a food of the redtail (see also Haddow in press). It is considered most unlikely that the swamp-forest activity peaks (Fig. 3*C*) were connected with the drinking of water by the redtail as it was never observed to drink, and its diet consists largely of fairly soft fruits.

When Figs. 3*C* and 9*D* are compared, it is found that the periods of greatest activity in the swamp forest coincide with the times when the proportion of bands is highest. It would be expected that activity would be high in the large social aggregations; the two main peaks of activity shown in the swamp forest may therefore be specifically connected with large group-size. The results presented in Fig. 5, showing that the early morning activity peak is strongly inhibited by heavy rain, agree with the observations of Haddow (in press). The combination of the feeding rhythm shown in Fig. 8 and the reduction of activity with increased temperature are probably the two factors responsible for the general shape of the main activity curve (Fig. 3*A*). So far as is known, no other activity rhythms have been published for diurnal tropical mammals, but the writer has found that a rhythm of this general type is common to several species of monkey in Uganda (personal observations).

The variations in proportions of the different group-sizes through the day are of interest, though reasons for these fluctuations are obscure. The relatively small size of sleeping parties implies that these were family units, as was suggested by Lumsden (1951). The fact that the mean band-size of sleeping redtails reported by him is significantly larger than that shown above does not affect this conclusion. The fluctuations in size of the diurnal aggregations of the redtail at different times of day and at times of day not particularly connected with feeding suggest that large troops and bands have a definite social function. It is possible that these assemblages, which are a very large proportion of the total population of the forest in one place at one time, are important in ensuring that the relatively small population contained in the forest is well mixed within itself, and not divided into small inbreeding units. The fact that there is no marked regularity from day to day in the size of groups seen in any one area suggests that, though the general social structure of the whole population may be constant at a given time of day, there is a certain amount of interchange between groups. This process is likely to go on when social aggregations are largest. No reason except established habit can be put forward to account for the fact that bands of redtails (over ten individuals) were seen more often from post X than in any other part of the forest. The largest single band seen consisted of twenty-five individuals.

The fact that group-sizes fluctuate during the day is a very strong indication that family groups do not maintain territories. Haddow (in press) produces evidence which

strongly suggests that territory does exist in redtail populations in large forest areas, but the territorial unit is large, probably an area about the size of Zika occupied by an equivalent redtail population. Carpenter (1942) and Causey, Laemmert & Hayes (1948) give information on the territorial habits of the Indian rhesus monkey, *Macaca mulatta* Zimmerman, and the South American monkey, *Cebus apella* (Linn.), respectively.

For the following reasons it is suggested that each individual redtail ranges at different times over a considerable area, if not over the whole forest. First, the number seen from any one post, or crossing a line of observers stretching across the forest, varied markedly between different days and weeks; secondly, large troops and bands were seen in several areas of the forest; thirdly, the extremities of the forest were not occupied by a resident population. These factors do not overrule the probability that a group may habitually live in one part of the forest rather than any other, which is strongly suggested by personal observation of tree routes used and by the times of waking in different areas (see p. 49).

The most usual group-sizes of various species of African monkey have been given by several authors, notably Zuckerman (1932) and Sclater (1900). Lumsden (1951) gives the mean and standard error of the size of sleeping groups for four species of monkey common in Mongiro Forest, Bwamba, Uganda, as well as some information on the sleeping habits of four other species in the same forest. These observations cannot be very closely compared with the present series from Zika owing to the different methods employed in each case. The observers in Zika were confined to making observations from one particular place in the forest, whereas Lumsden's observers moved about with the object of seeing exactly in which tree the monkeys were sleeping. Also, as explained above, the records made at Zika only show the direction and not the distance of the monkeys from the observer. The present observations do, however, agree with Lumsden's findings that the redtail is not a regular user of particular sleeping trees.

No previous work with which the population density of the redtail can be compared is known to the writer, but it may be deduced from Lumsden's paper that, in spite of considerable fluctuations, the density of the monkey population in Mongiro Forest while he was working there was of the order of three times as great as that found above for Zika Forest.

It is very probable that sexual activity in the redtail is confined to the hours of darkness when the monkeys are split up into small units, probably family groups. This contrasts strongly with the findings of Zuckerman (1932) with baboons. No direct evidence of the constitution of the normal redtail group is available but if, as seems likely, each group has a dominant male with one or more females and their young as was found by Zuckerman (1932) for baboons, the dominance of the male redtail must be of a different nature than that exercised by the male baboon. To account for the fact that all except one of the solitary redtails shot by him were adult males in good condition Haddow (in press) has suggested that there is a continual change-over of males in troops, spent males leaving troops and being replaced by rested ones. The only solitary redtail whose sex was positively identified in Zika during the present work was a female, identified by her conspicuous nipples, showing that she was either

lactating or was an old multiparous individual. The fluctuations in the percentage of solitary individuals seen at different times of day is probably due to the fact that they are not stimulated to activity by others and need not be active except when searching for food.

As this study was undertaken with a view to elucidating certain problems in the epidemiology of yellow fever, the results will be discussed briefly from this angle. First, from the evidence showing that each individual monkey may wander over a considerable area of the forest during the course of a few days, it is clear that monkeys alone are capable of disseminating a virus or other pathogenic organism throughout the biting-insect population of the forest canopy. Secondly, the difference in immune rates to yellow fever shown by the redtail and the grivet monkey (Haddow *et al.* in press) may be accounted for in two ways. Either the redtail, during its midday inactive period when it is in the forest canopy, is attacked by vector species of mosquito confined to the canopy which do not come in such close contact with the grivet monkey because the latter has different diurnal habits (personal observations), a possibility that has been fully discussed by Haddow *et al.* (in press), or the nocturnal sleeping habits of the two monkeys may account for their different immune rates. The frequency with which each monkey is bitten by a vector species* will affect its likelihood of being infected with the virus; the redtail is known to sleep in relatively small groups (see above, and Lumsden 1951), whereas the grivet has been found to sleep in groups of twenty or more in one tree very frequently (personal observations). Haddow (1942, 1945) has shown that the number of mosquitoes caught per man-hour is greater when a small bait of three or four people is used than if a large number are used. Relating these results to the habits of the two monkey species each individual grivet would be expected to be attacked by a smaller number of vector mosquitoes in a given time than each redtail.

To conclude this paper it seems worth while to reiterate its major conclusions in the form of a narrative of an imaginary typical day in the life of a group of redtail monkeys. The mean group-size of the whole population is four monkeys, and a typical family group probably consists of an adult male, one or two adult females, and one or two subadult or young. The group sleeps in the raised forest in fairly thick foliage, either in the lower part of the canopy of a mature forest tree, or in the upper branches of an understorey tree. The monkeys begin to wake up about 20 min. before sunrise, and are all very active and feeding by about a quarter of an hour after sunrise. The group is relatively inactive from about 0630 hr. sun time until 0745 hr. and not much feeding takes place, but some time during this period it moves into the swamp forest and becomes associated with other family groups to form large aggregations, often of over ten monkeys. While in these large groups activity increases considerably and a little feeding occurs. Some time between 0900 and 1030 hr. the large aggregations break up, probably into their constituent family units. These become gradually less and less active as the day grows hotter and rest in the thickest tree canopies, either in the raised or the swamp forest. Feeding ceases altogether between midday and 1330 hr. Sometime between 1330 and 1430 hr. activity and feeding starts again and the family

* The mosquitoes present in the forests of Bwamba are discussed by Haddow, Gillett & Highton (1947).

groups again congregate in the swamp forest, and often in a particular area. From 1500 to 1600 hr. most of the family groups in the forest are associated together in one large band, often of over twenty monkeys, so that any one redtail living in a group is probably associated with all the other redtails living in groups in the forest several times a week. Feeding occurs to some extent during this active period, and continues till sunset. Shortly after 1600 hr. the large band splits into its constituent family units which begin to leave the swamp forest and move towards the sleeping areas any time from 1700 hr. till sunset at 1805 hr. By sunset the majority of the family groups are back in the raised forest and in the neighbourhood of the sleeping areas, though still very active. All visible movement has ceased by 1825 hr., and the redtails are probably settled for sleep, though not in the same areas in which they woke up that morning.

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SUMMARY

1. The results of 1559 man-hours of observation on the redtail monkey, *Cercopithecus ascanius schmidti* Matschie, in Zika Forest, Mengo District, Uganda, are reported. The observations were carried out by Africans stationed in various parts of the forest.

2. It is shown that the redtail had a marked activity rhythm, and that this rhythm was different in the two forest types present at Zika. In the raised forest the activity peaks occur at approximately sunrise and sunset with little activity between, and in the swamp forest there are marked peaks at about 0800 and 1530 hr.

3. Heavy rain inhibits activity and high sun temperatures during the middle of the day reduce it.

4. The redtail feeds heavily at dawn, continues feeding through the morning till midday, and feeds again from about 1330 hr. till sunset. The majority of feeding occurred in the raised forest, but for reasons given the raised forest is not necessarily more important as a source of food than the swamp forest. A list of trees fed upon is given.

5. The size of the social groups of the redtail varied during the day. The solitary portion of the population varied at different times of day between 7 and 15% of the whole; small troops of 2, 3 and 4 monkeys predominated except at about 1400 hr. when large troops (5, 6, 7, 8, 9 and 10 monkeys) were at a maximum. Bands (over 10 monkeys) occurred principally at 0900 hr. and between 1400 and 1600 hr. The percentage of redtails occurring in each group-size was approximately the same for the first hour of observation as for the last hour, showing that sleeping units did not vary in size during the night.

6. The mean group-size for all observations was 3·0 monkeys. When solitary monkeys were excluded from the calculation the mean was 3·8 monkeys.

7. The mean number of adults per young in groups reported with young was 2·09. The probable constitution of the normal family group was one male, one or two females and none, one or two young.

8. The population of the redtails in Zika Forest was approximately 35, giving a density of one monkey per 1·3 acres.

9. The population was not distributed at random in the forest, areas of high canopy and no understorey growth being little occupied by the redtail.

10. The observation-rate at an observation post varied greatly on different days showing that the distribution of the monkeys within the forest varied on different days.

11. The redtails in Zika Forest do not occupy the same sleeping trees regularly. The mean size of probable sleeping groups is smaller in Zika than in Mongiro forest (Lumsden, 1951).

12. The social structure and behaviour within a redtail group is not so rigid or defined as that found by Zuckerman (1932) in two species of baboon.

13. The results are briefly discussed in the light of the epidemiology of yellow fever.

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THE 1951 CENSUS OF GANNETS (*SULA BASSANA*) ON AILSA CRAIG

By J. A. GIBSON

From 1936 to 1942 (Fisher & Vevers 1943) and again, after an unavoidable interruption during the war years, from 1947 to 1950 (Gibson 1951*b*) an annual census of gannets was carried out on Ailsa Craig. In 1940 the population was as high as 6232 pairs and in 1941 as low as 3518 pairs, but apart from these fluctuations the population remained remarkably steady, round a mean of about 5400 pairs, during the period 1936–49.

In 1950, however, the character of the colony changed abruptly, with a sudden increase of over 1500 pairs on the previous year's count, making a total of 6579 pairs—the highest population ever recorded for Ailsa Craig (Gibson 1951*a*). This represented certain colonization from without, possibly by birds that did not breed in previous years rather than by birds from another colony.

In June 1951 I repeated the census, using, as in former years, the method of direct counts of occupied nests, and was astonished to find a further increase of over 1250 pairs. The new group of nests first colonized in 1950 (Balvaar, Top Ridge) was again occupied, and fifteen groups held the highest population ever counted in any year, so that the 'population index' (see Gibson 1951*a*) is now 8777 pairs. Some diffusion has taken place among the north colonies, with the result that North of the Slunk, Foot of the Slunk and Above Ashydoo have more or less joined together, but the gannets have still shown no sign of spreading on to the sloping ground at the cliff-tops. The detailed counts for 1951 are given in Table 1.

We are now faced with the remarkable fact that the Ailsa Craig gannet colony has increased by nearly 3000 pairs since 1949. The reason for this increase is by no means clear, nor is it at all certain that the increase is permanent, but two possible explanations suggest themselves:

(1) Serious exploitation by man of the gannets on Ailsa has not been recorded since the 1880's, but Ailsa Craig probably suffered more than any other gannet colony from casual egg-collecting by visitors. The total number of eggs taken per annum may have been considerable. Since 1942, however, no egg-collecting of any significance has taken place, so it is possible that more birds were reared during these years and that the young birds, now mature, are returning to breed.

(2) Herring gulls and lesser black-backed gulls are notorious egg-thieves and cause considerable damage each season. In 1945 the population of gulls on the Craig was about 1500 pairs—far too many for the size of the island—so systematic destruction was then commenced (in 1950 it is unlikely that more than a few dozen young gulls were reared), and the population is now down to about 400 pairs. The proportionately less damage done to the gannets may therefore be an important factor in the increase.

Table 2 gives the detailed results from 1947 to date. The counts in 1947, 1948, 1950 and 1951 were made by J. A. Gibson, and in 1949 by J. A. Gibson, F. J. Huxley and H. G. Vevers.

Table 1. *Gannet pairs on Ailsa Craig in* 1951

Colony	Counts	Mean
Sliddery	235, 234, 239	236
Sliddery, Top Ridge	122, 122	122
North of the Slunk	277, 281	279
Foot of the Slunk	300, 301	300·5
Above Ashydoo	153, 151, 149	151
Balvaar	685, 669	677
Balvaar, Top Ridge	123, 123	123
Balvaar to Cairn	185, 188, 185	186
The Cairn	640, 641, 631	637·3
Cairn to Mare	403, 403	403
Barrheads	550, 559	554·5
Mare	1949, 1925	1937
Mare, Lower Ledge	63, 63, 63	63
Mare to Stranny Point, S 1	180, 180	180
Mare to Stranny Point, S 2	199, 204, 206	203
Mare to Stranny Point, S 3	218, 221	219·5
Mare to Stranny Point, S 4	342, 336	339
Stranny Point, South Side	43, 43, 43	43
Main Craigs, Main Part	407, 401, 405	404·3
Main Craigs, Top	442, 448	445
Main Craigs, East	183, 183, 186	184
Main Craigs, East Top	60, 60	60
Main Craigs, Far East	57, 57, 57	57
Main Craigs, Far East Top	29, 29	29

Total: 7833 pairs

Table 2. *The gannet population in recent years; all figures stand for the number of pairs*

Colony	1947	1948	1949	1950	1951
Sliddery	20	61	88	142	236
Sliddery, Top Ridge	73·5	60	84	203·5	122
North of the Slunk	429·3	202	124·3	175	279
Foot of the Slunk	311	181	159·75	207	300·5
Above Ashydoo	28·5	44	14	61	151
Balvaar	489	418	336·6	602·3	677
Balvaar, Top Ridge				120	123
Balvaar to Cairn	83	90	57·3	169	186
The Cairn	818	591	541·5	523	637·3
Cairn to Mare	277	*c.*500	674·5	345	403
Barrheads	235·5	*c.*250	202	430·5	554·5
Mare	1302	*c.*1500	1344·5	1823·5	1937
Mare, Lower Ledge	41	58	53	54	63
Mare to Stranny Point, S 1	91·5	102	108·6	175·3	180
Mare to Stranny Point, S 2	61	70	73	107·5	203
Mare to Stranny Point, S 3	131	*c.*150	160·3	209·5	219·5
Mare to Stranny Point, S 4	280	*c.*280	283·3	359	339
Stranny Point, South Side	12	21	22	39	43
Main Craigs, Main Part	229	211	202·3	228	404·3
Main Craigs, Top	305·5	255	275·3	409·5	445
Main Craigs, East	80·5	84	70·6	108	184
Main Craigs, East Top	9	17	15	28·5	60
Main Craigs, Far East	74	49	51·3	43	57
Main Craigs, Far East Top	2	6	6	16	29
Total by count	5383	2010	4947	6579	7833
Total by estimation	—	3180	—	—	—
Accepted grand total	5383	5190	4947	6579	7833

It has been estimated that the Ailsa Craig cliffs can hold easily 10,000 pairs of gannets (Gibson 1951*a*), but in fact it is unlikely that the population will ever reach this figure. The recent prospecting of Holy Island in the Firth of Clyde may be an indication that the gannets are already finding the Craig colony overcrowded.

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THE BROWN TROUT OF A MOORLAND FISHPOND

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(With Plate 1 and 7 Figures in the Text)

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INTRODUCTION

A biological survey of Three Dubs Tarn, a moorland fishpond in the Lake District was carried out over a period of years (1936–1947). Macan (1949) has published an account of the invertebrate fauna which he studied from 1936 to 1941 and 1947 to 1948. The age, growth and food of the brown trout of the tarn, based on data collected from 1936 to 1947, are the subjects of the present paper. In 1937 an experiment on this tarn was initiated by the Freshwater Biological Association to test the effect of adding bonemeal to the tarn on its general productivity. This experiment was only made possible by the kind and continued co-operation of the owner, Mr Maurice Illingworth. To him we are deeply indebted for giving us a free hand, help, and much local information. One aspect of the experiment, the growth of brown trout (*Salmo trutta* L.) before and after treatment as revealed by examination of their scales, was reported briefly in the annual report of the Association for 1940. The preliminary results of reading the scales of fish caught from 1936 to 1940, which was done by K. R. Allen, E. B. Worthington, G. Swynnerton and W. E. Frost, gave some reason to believe that the rate of growth of the trout was appreciably greater after than before treatment of the tarn with fertilizer. The analyses of results in the present paper, which cover the whole period (1936–1947) and which include a checking and revision of the earlier scale readings have, however, reduced considerably the emphasis which can be placed on the effect of the treatment with fertilizer on the growth of the trout.

The general features of the tarn have been described by Macan (1949) and only those presently relevant are noted here. Three Dubs Tarn (Pl. 1) lies at an altitude of

Photo: John Clegg

Three Dubs Tarn looking SSW to the dam.
[Reprinted from *J. Anim. Ecol.* **18**, Plate 7.]

700 ft. (215 m.) on Claife Heights, a range of fells lying to the west of Windermere. The tarn, which was made in 1908 by the erection of a concrete dam, has a surface area of 3·966 acres (16,066 sq.m.) and the greater part of the water is just over 10 ft. (3 m.) deep. The tarn is fed by six small streams, the two largest of which, 230 and 275 m. long, provide the only spawning grounds of the trout (p. 64). The bottom of the tarn is composed of a stiff black deposit of organic matter and boulder clay; there is a small stretch of stony shore on the north-east side of the tarn.

The distribution and changes in the higher plants have been fully described by Macan (1949). It was particularly noticed that a patch of *Potamogeton natans* was always present in the deeper waters and that *Nitella*, which was rare in 1936, had almost covered the deeper area of the tarn by 1944.

Chemically the tarn is a moorland water, poor in electrolytes and high in dissolved organic matter. In March 1937 Dr C. H. Mortimer determined the alkalinity as equivalent to 2·94 mg. $CaCO_3$ l.; after the bonemeal was added, in April 1937, an isolated alkalinity determined in August 1937 gave the figure 19·5 mg. $CaCO_3$/l. In a regular series of estimations of alkalinity and calcium made by Mr F. J. Mackereth in 1947–8 (Macan 1949) the 'alkalinity reached a maximum of 7·5 at the end of a long dry spell in August; a wet autumn brought it down to a minimum of 0·7, and it fluctuated round a value of about 2 throughout the winter. Calcium, unexpectedly, varied less. The maximum on 27 August was 5·2, and the minimum, on 26 February was 3·0 mg. l.' No regular temperature measurements were made, but surface readings showed 14·9° C. on 9 July, 20·7° C. on 27 August, 19·6° C. on 3 September 1947: after a long fine spell the temperature noted on 10 July 1949 was 25·6° C.

The invertebrate fauna and its seasonal changes are described in detail by Macan (1949), who showed that the most abundant organisms were the Chironomidae, *Pisidium*, *Leptophlebia* and the Corixidae; *Caenis* was fairly abundant and so were species of Odonata; Trichoptera were present all the year but their numbers were not so great as those of the other organisms. *Gammarus pulex* (L.) and *Limnaea pereger* (Müll.) were notably rare. Of the zooplankton random records only are available, and they show the presence but not the abundance of *Diaptomus gracilis* Sars, *Diaphanosoma brachyurum* (Lieven), *Ceriodaphnia reticulata* (Jurine) and *Cyclops* sp.

Bonemeal was added to the tarn on four occasions. In April 1937 50 kg. were scattered over half the area of the tarn surface; at the same time some limestone chippings were put into two of the small streams flowing into the tarn. In April 1939 and 1941, 50 kg. of bonemeal were scattered over the whole tarn, except in the region of very shallow water and the last application, of 20 kg., was in April 1944. The first period, 1936–41, of Macan's (1949) investigations covers the time before and after the first two bonemeal applications, and he suggests that during this period the effect of these treatments had been to increase the bottom fauna, well exemplified by *Pisidium*, by about ten times. Of the weed fauna he writes: 'That statistical analysis shows no increase in the fauna of the vegetation may be due to inadequate sampling but if there has been any increase it has been quite small.' He noted that the spread of the growth of *Nitella* enabled some dragonfly nymphs and larval Trichoptera to extend their range, and that *Cloëon* was more abundant than it was originally, he added that the population of Corixidae and Gastropoda was still that typical of

a base-deficient moorland tarn. Macan's observations refer to the period 1936–41, and there is no information on the effect on the invertebrates of the addition of bonemeal in 1941 and 1944.

The original fish stock, when the tarn was made in 1908, consisted of those trout present in the beck which was dammed to form the tarn, and of individual trout caught in local becks and transferred to it. In 1936 Mr Illingworth acquired the tarn, and in May 1937 he put in 100 brown trout of 3–5 in. long (7·5–12·5 cm.). In April 1938 fifty American brook trout (*Salvelinus fontinalis* (Mitchill)) were added; no further stocking has been done and no other fish were present. None of the brook trout was ever taken in the annual nettings, and after 1939 none was taken by rod. It therefore seems likely that they did not survive very long and may be discounted as part of the fish fauna.

The stock of trout is maintained by natural propagation. The trout spawn in the lower 50–70 yd. (45–65 m.) only of each of the two main streams, each about 0·5 m. wide, as access to their upper parts is prevented by small but insurmountable waterfalls. Fingerling fish of 2·3–2·5 cm. long have been found in the streams in April and May, but no yearlings were seen on these visits or in November when adult trout were in the beck for spawning.

METHODS

Although a few fish were rod-caught, the majority from 1936 to 1947 were taken by seine in the spring of each year. Until 1944, the net used was 50 yd. long, 6 ft. deep and had a mesh of 1 in.; in 1944 and subsequently, a net of 2 in. mesh was used. The seine was drawn until, if possible, at least fifty fish were caught, this usually meant three to five drafts which covered about half the area of the tarn. The fish caught were returned alive after each had been measured to 0·5 cm. below and weighed to the nearest gram, and a sample of scales had been taken from it. Sex was noted only for those few fish which died and could be examined internally, and the stomachs of these were also examined. The fish taken by angling were caught from April to September in various years, the month and year of capture depending on opportunity; all were caught on the wet or dry fly. These trout were usually weighed, measured, sexed and the stomach contents examined, and in some instances samples of scales were taken. As the sex was determined in a few instances only, it was impossible to determine the sex-ratio of the fish caught and all the results given on size, age and growth refer to fish irrespective of sex.

The food of the trout was determined from the examination of the stomach contents of 182 fish caught by seine and angling with wet and dry fly in the months of March to September 1939–49. The food organisms in the cardiac and pyloric parts of the stomach were counted and identified, some to species. The capture of fish did not coincide with the times of faunistic collections by Macan (1949), and as the fish were those individuals of the annual seining which happened to die and others taken on various angling occasions it is likely that there has been some selection of the specimens. Therefore, although for comparative purposes the data on fish and fauna are not ideal, they present an opportunity for a comparison which, as it seldom occurs, will be taken.

The age of each fish and the length attained at the end of each year of life were determined from scales. In some scales, particularly of older fish, there was difficulty in determining the position of the first winter band. In most scales this was a well-defined band of narrow circuli which was calculated to correspond to a length of about 10–12 cm. In some scales there was between this band and the centre an ill-defined check consisting of one or two circuli set somewhat closer together than the others. The calculated length corresponding to this point was 5–7 cm. In 1940 among 28 trout determined as 1-year-old and having a mean observed length of 10·8 cm. there were individuals whose scales showed the ill-defined check at 5–7 cm. This supported the opinion that on those scales showing the two checks the true first winter band was that at 10–12 cm., not at 5–7 cm., and it was concluded that the latter was a check associated with the change from life in the beck to that in the tarn. There are, however, some scales in which the check at 5–7 cm. is represented by a well-defined group of narrow circuli followed by a series of wide ones typical of summer growth and thus appears to indicate the first winter. Probably the fish showing this winter band had descended to the tarn later in the season and made less growth than those others which descended earlier and attained 10–12 cm. by their first winter.

FOOD

Of 182 trout examined, the stomachs of 177 contained food and in no month was there more than one empty individual. In Table 1, which shows the organisms eaten each month, a distinction is made between the submerged and surface foods. The submerged food organisms all originated in the tarn with the exception of 'Miscellaneous organisms' which contained plant debris and moss capsules as well as one newt and the bones of a frog. The surface foods are subdivided into those of aquatic and terrestrial origin, the latter category consisting chiefly of Aphidae, Diptera and Coleoptera. Macan (1949) gives the specific names of nearly all the animals occurring in the tarn, and the species in Table 1 may be identified from his paper. From the data in Table 1 the seasonal variations in the food of the trout are deduced, it must be borne in mind that the number of fish and manner of their capture varied each month.

March	The fish are feeding on weed and bottom-dwelling invertebrates, chiefly Trichoptera larvae, Ephemeroptera nymphs and *Pisidium*; the preponderance of *Sialis* is unexpected and inexplicable.
April	Chironomid pupae, which are beginning to emerge in large numbers, are the main food.
May	Winged insects of both terrestrial and aquatic origin are added to the diet and take second place only to chironomid pupae. Weed and mud-living organisms, particularly larvae of Trichoptera and *Pisidium*, were preyed upon to a large extent.
June	Winged insects, chiefly terrestrial, leptocerid larvae, chironomid pupae and *Caenis* nymphs are all important foods. The nymphal *Caenis*, which are now ascending to the surface to emerge as adults, suddenly leap into prominence in the diet. One trout caught in June contained nothing except one newt.
July	The main foods are larval leptocerids and chironomids, the pupae of chironomids and nymphs of *Caenis*, all organisms which were taken below the surface. The nymphal *Caenis* were all found in four trout caught during an emergence of this species.
August	Foods taken below the surface, Trichoptera and chironomid larvae and pupal chironomids, are important in the diet, and there is some surface feeding on terrestrial insects and winged Trichoptera.

September — Surface food predominantly of terrestrial origin, winged Diptera, aphids, etc., occurs in a high proportion of the trout. Considerable numbers of mud- and weed-living organisms are eaten; the variety of species suggests that food is becoming less easy to find.

Macan (1949) deduces from his faunistic studies which animals will be available for the fish to eat in the different seasons, and the data presented above show that the trout feeds, in the main, on what Macan said was available. There are, however, certain exceptions. Trichopterous larvae, particularly *Leptocerus*, feature more prominently in all months than might be expected from the faunistic records. There is no explanation why the proportion of *Sialis* eaten in the month of March is so high. It is evident that the trout of Three Dubs Tarn eat no frog or toad spawn nor any tadpoles. The highest

Table 1. *Food of trout in Three Dubs Tarn shown as the number of fish feeding on a food expressed as a percentage frequency of the number containing food (% F) and as the average number of organisms per fish (av.)*

(The symbol + indicates <0·1.)

	March		April		May		June		July		August		Septemb	
No. of fish examined	37		9		31		27		18		15		45	
No. containing food	36		8		30		26		18		14		45	
Mean length of fish (cm.) ...	18·0		23·6		24·8		24·2		22·7		21·3		24·2	
Assessment of food	% F	Av.	% F	Av.	% F	Av.	% F	Av.	% F	Av.	% F	Av.	% F	A
SUBMERGED AQUATIC:														
Leptocerus, larvae	33	1·2	25	1·5	77	10·7	35	5·5	45	4·9	50	4·2	11	0
Polycentropid larvae	25	0·3	·	·	6	+	19	0·5	·	·	·	·	9	0
Limnophilid larvae	36	1·3	·	·	27	0·5	·	·	11	0·5	·	·	2	
Oxyethira, larvae	11	0·3	·	·	6	0·1	·	·	·	·	·	·	·	
Trichoptera larvae indet.	17	0·1	12	0·4	·	·	15	0·7	·	·	7	0·1	4	0
Trichoptera pupae	·	·	·	·	·	·	·	·	·	·	21	0·2	4	
Leptophlebia, nymphs	50	1·4	12	0·8	33	2·3	·	·	·	·	·	·	·	
Caenis, nymphs	·	·	12	0·8	3	+	35	7·6	22	7·7	·	·	·	
Ephemeroptera, nymphs indet.	·	·	·	·	3	0·6	12	0·1	·	·	·	·	3	
Chironomid larvae	28	2·5	50	6·0	23	1·2	15	2·6	33	3·0	43	2·0	22	0
Chironomid pupae	·	·	62	35·6	57	5·8	42	4·7	45	3·7	57	1·1	35	1
Tipulid larvae	·	·	·	·	·	·	4	+	·	·	·	·	·	
Odonata nymphs	22	0·4	37	2·6	33	0·9	27	1·6	5	0·2	7	+	20	0
Sialis lutaria, larvae	77	4·6	37	1·0	3	+	8	+	5	+	21	0·3	31	0
Coleoptera imagines	·	·	·	·	10	0·1	·	·	5	+	·	·	2	
Coleoptera larvae	3	+	·	·	7	+	8	0·1	·	·	·	·	4	
Corixidae	3	0·1	·	·	3	0·5	23	0·5	5	0·3	7	+	18	0
Gerris lacustris	·	·	·	·	·	·	·	·	·	·	·	·	2	
Hydracarina	·	·	·	·	3	+	·	·	·	·	·	·	·	
Pisidium	30	1·2	37	0·8	33	8·7	12	0·2	·	·	7	0·2	16	0
Limnaea pereger	5	0·2	12	1·5	·	·	·	·	5	0·5	·	·	9	0
Gammarus pulex	·	·	·	·	·	·	·	·	5	+	·	·	·	
Diaphanosoma brachyurum	·	·	12	2·5	·	·	·	·	·	·	·	·	26	0
Eurycercus lamellatus	11	10·0	·	·	·	·	·	·	·	·	·	·	·	
Fish	·	·	·	·	·	·	·	·	5	+	·	·	·	
SUBMERGED AQUATIC AND TERRESTRIAL:														
Miscellaneous organisms	2	0·1	12	0·1	17	0·2	4	+	·	·	·	·	4	
SURFACE AQUATIC:														
Trichoptera	·	·	·	·	·	·	8	0·3	5	+	36	0·8	11	0
Ephemeroptera	·	·	·	·	23	0·9	15	1·1	·	·	·	·	·	
Diptera	·	·	25	0·9	7	0·2	4	0·2	·	·	7	+	·	
Odonata	·	·	·	·	3	+	·	·	·	·	·	·	·	
Plecoptera	·	·	·	·	·	·	·	·	·	·	·	·	4	
Sialis lutaria	·	·	·	·	27	0·5	4	+	·	·	·	·	·	
SURFACE TERRESTRIAL:														
Aphidae, Diptera, Coleoptera	·	·	12	0·6	54	4·3	61	4·6	17	0·6	29	1·8	71	4

figure for consumption of planktonic animals occurs in April, and this may be related to the fact recorded by Macan that in this month these animals 'begin to increase', but there are no quantitative seasonal data for zooplankton on which this correlation can be based or the virtual absence of plankton in the diet at other times explained. In the autumn months when 'chironomids are much reduced in numbers' they are eaten by many fish and in good numbers in August; in September half of the fish were feeding on them. These exceptions suggest that the diet of the trout is not wholly determined by what is available but that they exercise some selection. Further light on the extent to which the trout selects its food is obtained by comparing the relative proportions of each organism in the fish and in the fauna. In Table 2 the faunistic

Table 2. *Comparison of food organisms eaten by trout with those present in the fauna of Three Dubs Tarn*

	Spring		Summer	
No. of feeding fish	74		77	
Mean length (cm.)	21·3		23·3	
	Nos. eaten	Nos. in fauna	Nos. eaten	Nos. in fauna
MUD-LIVING ORGANISMS:				
Chironomid pupae	461	·	135	·
Chironomid larvae	176	4158	113	1284
Sialis lutaria, larvae	177	32	29	39
Caenis, nymphs	1	386	140	1
Pisidium	312	1032	38	713
Oligochaeta	·	49	·	52
TOTAL MUD-LIVING ORGANISMS	1127	5657	455	2089
WEED-LIVING ORGANISMS:				
Leptocerus, larvae	374	3	149	34
Limnophilid larvae	62	31	10	33
Polycentropid larvae	12	54	11	25
Leptophlebia, nymphs	126	242	·	1
Odonata nymphs	61	59	14	130
Coleoptera imagines	4	2	3	9
Corixidae	19	203	17	227
Limnaea peregra	21	4	34	8
Hydracarina	1	86	1	92
TOTAL WEED-LIVING ORGANISMS	680	684	239	559
Hirudinea	·	3	·	33
Gammarus pulex	·	18	1	3

data from tables 3 and 7 of Macan (1949) are set out for this purpose, the figures for individual collections in Macan's tables 3 and 7 having been totalled and the results added together. These results were based on hauls taken by a specially designed hand-grab and by a Peterssen grab, and although the number of such hauls was small no big variations of any one species of animal was found in the different years. Macan's samples taken from February to March and from July to August are compared with the food of trout from March to May and from July to September respectively. On this basis the data are presented as 'spring' and 'summer' in Table 2, the organisms living in the mud being divided from those living in the weed.

It is convenient to begin the comparison of food and fauna with the nine species in the table, which are more prominent in the fauna than in the food. The total of 18

Gammarus pulex does not give a true picture, since all occurred in one haul, and Macan believes that they came down from a nearby beck. The number of corixids eaten is low in spite of their abundance in the fauna; this is not unexpected for there is evidence that this common animal is not usually acceptable to trout (Frost & Macan 1948). Examination of trout stomachs from other waters shows that Hydracarina and Hirudinea are seldom eaten, but that polycentropid larvae are readily consumed, and it is not apparent why more were not taken by the trout of Three Dubs Tarn. There remain *Caenis*, chironomid larvae, *Pisidium* and oligochaetes; all these are mud-dwellers and presumably owe to this habitat their relative immunity. When, however, in July and August *Caenis* leaves the mud and ascends to the surface to emerge, the trout eat it in great numbers, as is seen by the summer figures. Chironomids too are eaten readily, when as ascending pupae they launch into the open water. Good numbers of *Pisidium* are eaten perhaps because, although a mud-dweller, this animal often lies on the surface of the mud and is probably obtained fairly easily; it is more heavily grazed in spring and summer time. No oligochaetes were found in the trout stomachs.

Of those animals that are more prominent in the food than the fauna only one, *Sialis*, is a mud-dweller. This as already noted is eaten in large numbers in March and April; whether or not there is anything about its behaviour that would account for this is not known. There is great disparity between the numbers of larval *Leptocerus* in stomachs and fauna, and it must be concluded that these larvae are sought assiduously by the trout. The figures for the remaining animals suggest that the extent to which they are eaten depends on their abundance. Zooplankton plays a remarkably small part in the diet. The Three Dubs trout are not piscivorous, probably because there are no forage fish in the tarn and few of the trout are large enough to be cannibals. The importance of terrestrial animals blown on to the surface is clear.

In Table 3 the food of 177 trout is arranged to show that of small and large fish; the percentage number of the total fish examined (small 56, large 121) feeding on each organism is given. Small trout are those of 20 cm. and less in length, the remainder are large ones. Appreciably more small than large fish feed on chironomid larvae and *Leptophlebia* nymphs, but there are twice as many large as small fish feeding on surface organisms of terrestrial origin. Apart from this there is practically no difference in the diet of the two sizes of trout.

There is the question of the actual amount of food in Three Dubs Tarn and its relationship to that eaten by the trout. Macan (1949) estimated the mud fauna, consisting chiefly of *Pisidium*, chironomid larvae and *Sialis* larvae, of a typical Lake District fishpond (an estimate based on data from four similar tarns, near to Three Dubs, which had not been interfered with by addition of bonemeal) as between 1000 and 2000 organisms per square metre, and refers to these figures as 'unexpectedly high when compared with those quoted by Berg (1938)'. After the bonemeal treatment of Three Dubs Tarn there was an increase in the mud fauna which Macan tentatively estimates as about tenfold, and the number of animals was then nearly as high as in some of the most productive lakes investigated by Berg. Of the weed-dwelling organisms in Three Dubs Tarn Macan says (1949, p. 179) that 'this is a small population' consisting of about 300 animals per square metre, excluding

chironomids; this population was still small after treatment by bonemeal and, it can be taken, from Berg's (1938) figures, that productive lakes may contain ten times this amount. This abundance of mud-living organisms and comparative scarcity of weed-living ones is seen also from the totals of each type for 'Spring' and 'Summer' faunas in Table 2, while comparison of these figures with similar totals for the numbers eaten by the fish shows that more weed than mud animals are eaten in relation to their respective numbers in the fauna. From Table 3 it will be seen that, apart from chironomid larvae (mud-dwellers), and *Leptophlebia* (a weed-liver), mud- and weed-living animals are eaten to much the same extent by both large and small trout. Thus Three Dubs Tarn has an abundant mud fauna and a scarce weed fauna, but in relation to numbers present the weed animals are more heavily grazed by the trout and also mud and weed organisms are cropped equally by both large and small trout.

Table 3. *Food of small and large trout*

	Percentage of fish feeding	
	Fish (56) under 20 cm. long	Fish (121) over 20 cm. long
MUD-LIVING ORGANISMS:		
Chironomid pupae	37	39
Chironomid larvae	59	17
Sialis lutaria, larvae	37	23
Caenis, nymphs	2	9
Pisidium	26	18
WEED-LIVING ORGANISMS:		
Trichoptera, larvae (chiefly *Leptocerus*)	55	50
Leptophlebia, nymphs	34	7
Odonata nymphs	23	21
Coleoptera imagines	9	7
Corixidae	11	17
Limnaea pereger	4	5
Hydracarina	1	1
MID-WATER ORGANISMS:		
Zooplankton	11	7
Fish	·	1
SURFACE ORGANISMS OF TERRESTRIAL ORIGIN	25	46

POPULATION AND MORTALITY

No definite information about the trout population of the tarn is available. Marking experiments in 1940 and 1941 when 65 and 58 fish were tagged gave no assessment of population as none of the marked fish was ever caught either by seine or rod. Annual fluctuations in the number of fish in the tarn may perhaps be indicated by the numbers taken in the yearly seine hauls (Table 4), since approximately the same seining effort, resulting in about half the tarn being fished, was carried out each year, but the figures cannot be regarded as absolute and can be taken only as giving a rough estimate of fluctuations of the population. There is little information to explain the wide variation in the numbers seined each year. In March 1944 the net was badly tangled by *Nitella* which had then reached maximum growth and this probably accounted for the low number of fish caught that year, as in June when a larger mesh seine was used 65 trout were caught. Early in 1944 it was suspected that otters were fishing the tarn and two were caught in October. Their depredations may explain the low catches of 1944 and

1945. The population may have been affected by the water conditions in the two spawning streams, for drought or spate during the late spring and early summer would affect the survival-rate of fry.

Table 4. *Number and size of trout taken in Three Dubs Tarn in each year's seine collection*

	No. caught	Mean length (cm.)	Mean weight (g.)
July 1936	32	19·0	112
Mar. 1937	15	14·1	148
Sept. 1938	76	20·8	133
Mar. 1939	99	22·8	133
Mar. 1940	118	18·1	105
Mar. 1941	154	19·1	87
Apr. 1942	85	20·4	98
Mar. 1943	92	22·2	130
Mar. 1944	19	25·7	154
Apr. 1945	58	26·5	175
Apr. 1946	52	25·6	204
Apr. 1947	79	21·8	124

An idea of the relative population of the year-classes over the period 1936–47 is obtained from Table 5 where the numbers of trout (only seine-caught fish) of each year-class is given. Differences in the time of survival of the different year-classes and the number of fish of each age that survived result in great variation in the population of the year-classes. The relative size of these year-classes in relation to their growth is discussed later (p. 81).

Table 5. *Results from age determinations arranged to show the number of trout of each age in each annual seine collection of fish, and the number of trout caught of each year-class*

Year of collection	Age of fish (years) 1	2	3	4	5	6	7	8	Total: all ages	Year-class	No. caught
1936	9	1	8	4	·	·	·	·	22	1935	53
1937	2	2	2	6	3	1	·	·	16	1936	51
1938	28	16	19	5	1	·	·	·	69	1937	79
1939	3	26	27	16	11	6	·	1	90	1938	111
1940	43	44	19	5	3	1	·	·	115	1939	211
1941	1	73	47	6	·	3	1	·	131	1940	85
1942	1	13	50	14	·	1	1	·	80	1941	39
1943	·	5	43	37	2	·	·	·	87	1942	32
1944	·	·	4	13	2	·	·	·	19	1943	27
1945	·	4	18	16	11	3	1	·	53	1944	13
1946	·	5	17	12	10	4	2	·	50	1945	50
1947	5	50	8	6	2	3	·	1	75	1946	5
Total fish 1936–47	92	239	262	140	45	22	5	2	807		

The survival rate of fish of different ages is estimated from the age-frequency data given in Table 5 by expressing the number of fish in an age-group as a percentage of the number in the preceding group. In this way the estimation of the survival-rate during the 3rd to 4th year is 53%, 4th to 5th year 32%, 5th to 6th year 46%, 6th to 7th year 23% and 7th to 8th year 40%; the rate for fish of 1–3 years old is not

computed, as the number caught is obviously fewer than would be actually present, probably owing to net selection. The high survival-rate (53%) during the 3rd to 4th year suggests that it may be due to the fish being immature and that spawning may be a factor contributing to the lower survival-rate of subsequent years, but even so there are no violent changes in the rate of survival in these years. An overall survival-rate from the 4th to 8th year is given by Fig. 1 in which the data in Table 5 are

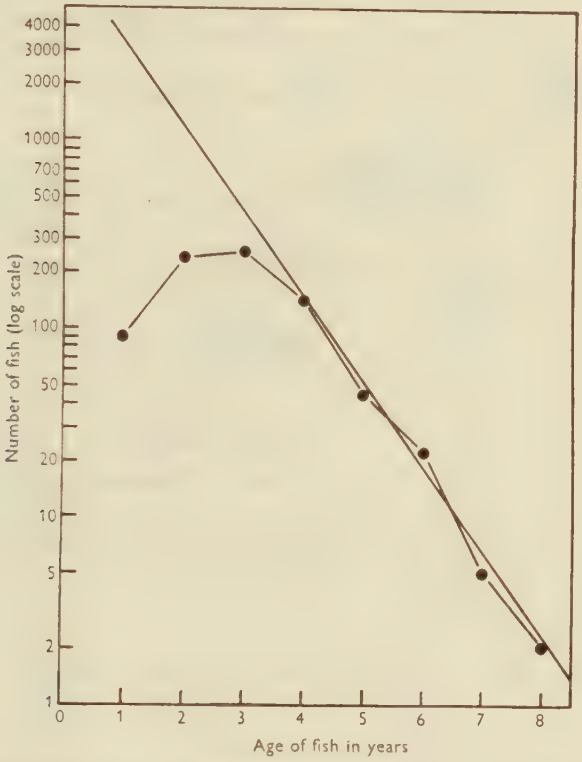

Fig. 1. Survival rate of trout of different ages. The regression line (drawn by eye) corresponds to a uniform survival rate of 35%.

plotted on a logarithmic scale and a line drawn by eye through the points for fish of 4–8 years old. The steepness of the slope of this line and the figure of 35% which is that for the overall survival-rate deduced from it, indicates a fairly high survival of fish of 4–8 years old.

SIZE, AGE AND GROWTH

The length-frequency distribution of each year's collection of fish, based on 886 seine-caught trout, is shown in Fig. 2, and Table 6 shows the size of the trout of any age for each year's collection. The age-frequency distribution of the fish collected in each year is given in Table 5 and Fig. 3. Comparison of Fig. 3 with that for the length-frequency distribution (Fig. 2) shows that the pattern of variation in the collections of the different years is much the same for age and length, a coincidence which lends support to the estimates of age made from the scales.

The size and age of the fish in relation to sex or sexual condition was difficult to determine since few trout were examined internally, and examination of the scales for

spawning marks, although sometimes informative, did not always give satisfactory results. Such evidence as was available from examination of gonads and scales indicated

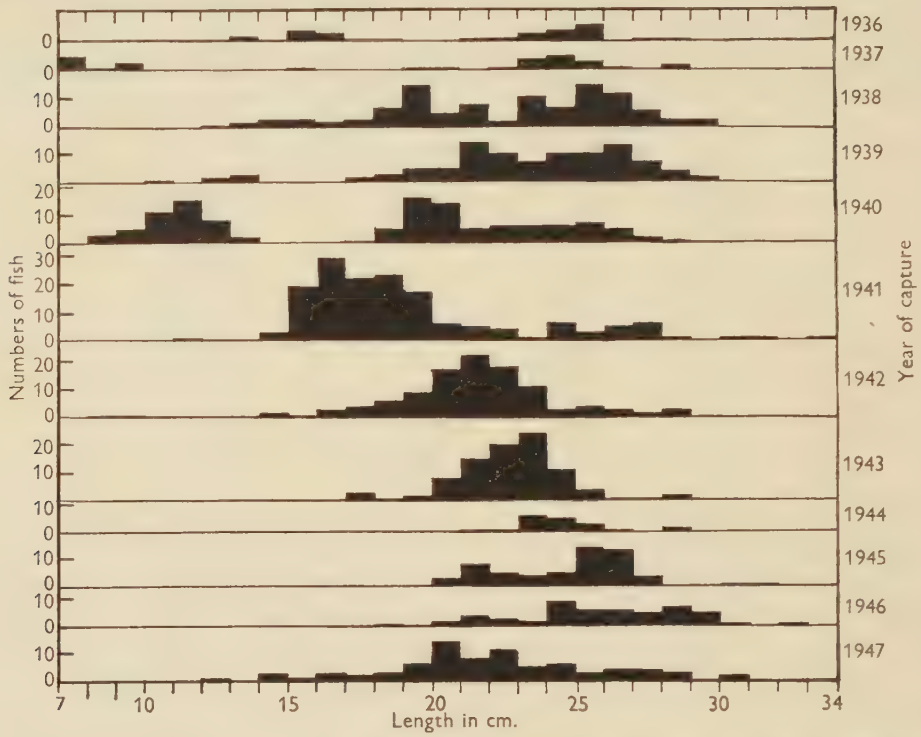

Fig. 2. Distribution of length among 886 trout caught by seine in Three Dubs Tarn from 1936 to 1947.

Table 6. *Mean length-for-age of trout from each year's collections, and mean weight of the 780 fish weighed*

(Numbers of fish are given in brackets.)

Year of collection	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	Mean length all fish (cm.)	Mean weight of those fish weighed (g.)
Length at end of:														
1st year	7·5	7·8	8·0	7·8	10·1	9·0	8·7	9·1	9·4	8·1	7·5	8·1	8·6	59
	(22)	(16)	(106)	(90)	(115)	(131)	(101)	(87)	(19)	(53)	(50)	(75)	(865)	(52)
2nd year	16·5	17·4	16·8	16·6	19·7	17·4	17·7	18·0	18·9	19·0	19·6	19·9	18·1	92
	(13)	(14)	(76)	(87)	(72)	(130)	(100)	(87)	(19)	(53)	(50)	(70)	(771)	(241)
3rd year	20·7	21·1	21·5	22·1	23·7	19·5	20·9	21·6	22·6	22·5	23·9	23·4	21·8	126
	(12)	(12)	(41)	(61)	(28)	(57)	(81)	(82)	(19)	(49)	(45)	(20)	(507)	(277)
4th year	22·6	23·7	23·9	24·7	24·8	23·6	22·8	22·9	24·0	24·8	26·2	25·6	24·2	162
	(4)	(10)	(15)	(34)	(9)	(10)	(19)	(39)	(15)	(31)	(28)	(12)	(226)	(135)
5th year	·	24·9	22·9	26·0	26·3	24·9	25·1	25·5	25·5	25·8	27·6	26·4	26·1	202
		(4)	(2)	(18)	(4)	(4)	(4)	(2)	(2)	(15)	(16)	(6)	(77)	(47)
6th year	·	25·8	·	27·0	26·3	26·3	27·0	·	·	26·9	28·3	27·6	27·2	210
		(1)		(7)	(1)	(4)	(2)			(4)	(6)	(4)	(29)	(21)
7th year	·	·	·	26·0	·	25·5	27·0	·	·	26·5	29·3	29·9	27·6	215
				(1)		(1)	(1)			(1)	(2)	(1)	(7)	(5)
8th year	·	·	·	26·9	·	·	·	·	·	·	·	30·5	28·7	213
				(1)								(1)	(2)	(2)
No. of fish examined	22	16	106	90	115	131	101	87	19	53	50	75	865	780

that the majority of the trout spawned for the first time at the end of their 4th year of life, but that a few individuals spawned when 3 years old. All the results given in this paper refer to the trout regardless of the sex of the fish.

The age and growth of the trout have been determined from 865 individuals, of which 807 were caught by seine and 58 were taken by angling. The mean length-for-age of fish in each year's collection is shown in Table 6, which includes a summary of the weight-for-age for the 780 trout from all collections. The means for all fish, length and weight, have been plotted in Fig. 4 to show the general pattern of growth

Fig. 3. Distribution of age among 886 trout caught by seine in Three Dubs Tarn.

in Three Dubs Tarn. The trout grew fastest during the first 3 years of life, remarkably quickly during the first 2 years but a little slower in the third, then at a steadily declining rate. This pattern is expressed in terms of annual increments and specific growth-rate (calculated from the formula given on p. 79) in Table 7. The specific growth-rate is highest in the first 2 years of life, notably high in the 1st year, and the increment made during the 2nd year of life (9·5 cm.) is so large as to mask the effect of the marked fall of the specific growth during the 3rd year; subsequently annual increments and specific growth fall rapidly.

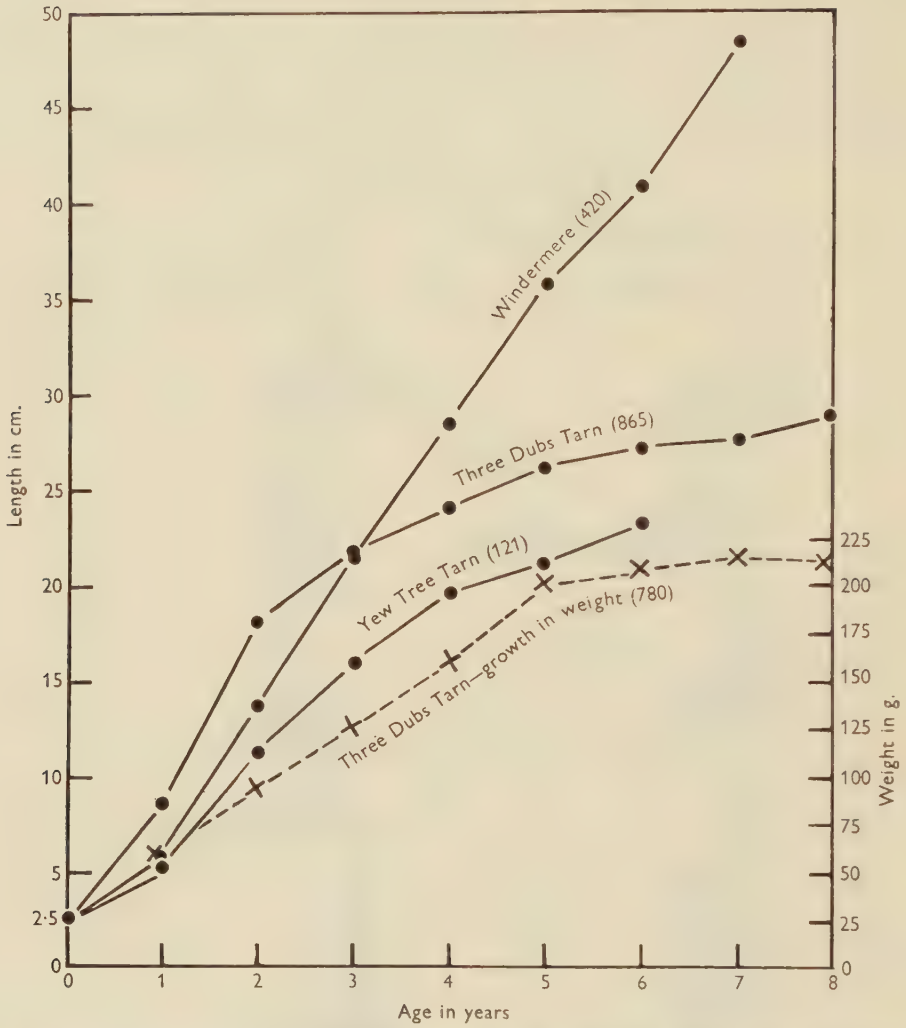

Fig. 4. General pattern of growth in length of trout from three waters in English Lake District; growth in weight also given for Three Dubs Tarn. (Number of fish given in brackets.)

Table 7. *Growth, annual increments and specific growth-rate of trout from Three Dubs Tarn, Windermere and Yew Tree Tarn*

Length (cm.) after:	Three Dubs Tarn	Windermere (Allen 1938)	Yew Tree Tarn (Swynnerton & Worthington 1939)	Years	Annual increments and specific growth-rate: Three Dubs Tarn Increment (cm.)	Three Dubs Tarn Specific growth-rate	Windermere Increment (cm.)	Windermere Specific growth-rate	Yew Tree Tarn Increment (cm.)	Yew Tree Tarn Specific growth-rate
1 year	8·6	5·8	5·2	0–1	6·1	123	3·3	84	2·7	73
2 years	18·1	13·7	11·2	1–2	9·5	74	7·9	85	6·0	76
3 years	21·8	21·5	16·0	2–3	3·7	19	7·8	45	4·8	35
4 years	24·2	28·5	19·7	3–4	2·4	10	7·0	28	3·7	21
5 years	26·1	35·8	21·3	4–5	1·9	7	7·3	22	1·6	7
6 years	27·2	40·8	23·2	5–6	1·1	4	5·0	13	1·9	8
7 years	27·6	48·3	•	6–7	0·4	1	7·5	16	•	•
				7–8	1·1	3	•	•	•	•

(*a*) *Variations in age and growth*

Consideration of the variations in age and growth of the trout over the period 1936–47 is based on results given in Table 8 which are expressed graphically in Figs. 5 and 6; in Fig. 5 the mean length attained for age is shown, in Fig. 6 the growth of each year-class is presented. In Table 8 each section deals with fish of one age, e.g. '1 year old', which means fish which have completed 1 year of life as determined from the scales. Each 'grand mean' has been obtained from fish which were living contemporaneously and therefore under the same conditions in the tarn; such a mean takes

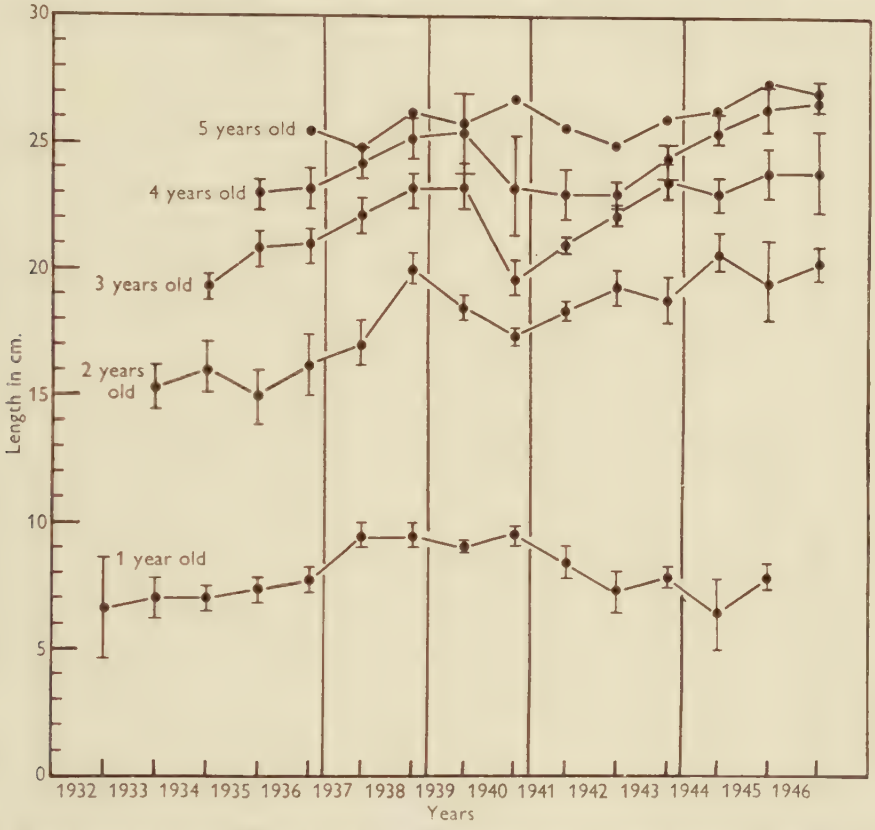

Fig. 5. The growth of trout in Three Dubs Tarn. The mean length-for-age attained by fish of 1–5 years old in the different years 1932–46; twice the standard error of the mean is shown. The times of addition of bonemeal to the tarn are indicated by vertical lines.

into account the year-class, noted in the left-hand vertical column and the date of capture of the fish noted in the top horizontal line. How a 'grand mean' is obtained is best explained by an example. Thus the grand mean for 2-year-old fish of the 1937 year-class is 20·1 cm. It has been obtained from four means, 20·5, 20·3, 19·4 and 15·6 cm.; the mean 20·5 is based on observed lengths (in heavy type) because as the 26 fish were captured in 1939 they were actually 2 years old when measured, whereas the other three means are based on lengths back-calculated from scales as they were from fish captured in 1940, 1941 and 1942, fish which had lived for 3, 4 and 5 years respectively; thus although based on fish of 2, 3, 4 and 5 years old, the grand mean is that

Table 8. *The growth of trout in Three Dubs Tarn at different ages arranged in year-classes*

(Each entry shows the mean length in cm. of the number of fish which follows in brackets. Figures in heavy type refer to observed lengths, others to lengths estimated from scales. For further information see text p. 75.)

Year-class	Year of capture												No. of fish	Grand mean and S.E.
	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947		
One-year-old fish														
1945	.	.	.	.	.	.	.	.	.	.	.	7·9 (50)	50	7·9 ± 0·25
1944	.	.	.	.	.	.	.	.	.	.	5·0 (5)	7·3 (8)	13	6·4 ± 0·69
1943	.	.	.	.	.	.	.	.	.	7·2 (4)	7·4 (17)	9·8 (6)	27	7·9 ± 0·39
1942	.	.	.	.	.	.	.	.	.	7·3 (18)	7·7 (12)	5·5 (2)	32	7·3 ± 0·40
1941	.	.	.	.	.	.	**9·0** (1)	8·2 (5)	9·3 (4)	8·9 (16)	8·0 (10)	7·5 (3)	39	8·5 ± 0·29
1940	.	.	.	.	.	**11·5** (1)	8·8 (19)	9·9 (43)	9·8 (13)	9·0 (11)	9·0 (4)	.	91	9·5 ± 0·21
1939	.	.	.	.	**10·8** (28)	9·0 (73)	8·7 (62)	8·4 (37)	7·3 (2)	6·6 (3)	8·4 (2)	6·0 (1)	223	9·1 ± 0·12
1938	.	.	.	**12·0** (3)	10·0 (44)	9·0 (47)	9·2 (15)	7·2 (2)	.	6·4 (1)	.	.	112	9·4 ± 0·19
1937	.	.	**9·8** (30)	9·1 (26)	9·9 (19)	8·5 (6)	7·5 (2)	.	.	.	.	.	83	9·4 ± 0·22
1936	.	**6·8** (2)	8·0 (35)	7·2 (27)	7·2 (5)	.	10·0 (1)	.	.	.	.	.	70	7·6 ± 0·24
1935	**8·1** (9)	9·4 (2)	6·6 (26)	7·0 (16)	8·8 (3)	9·0 (3)	6·7 (1)	.	.	.	.	.	60	7·3 ± 0·27
1934	7·4 (1)	8·5 (2)	7·0 (13)	6·9 (11)	7·0 (1)	5·0 (1)	.	.	.	.	.	.	29	7·0 ± 0·27
1933	7·3 (8)	7·8 (6)	3·8 (2)	6·7 (6)	.	.	.	.	.	.	.	.	22	7·0 ± 0·42
1932	6·5 (4)	6·8 (3)	.	.	.	.	.	.	.	.	.	.	7	6·6 ± 1·01
1931	.	7·3 (1)	.	6·0 (1)	.	.	.	.	.	.	.	.	2	6·7
Two-year-old fish														
1945	.	.	.	.	.	.	.	.	.	.	.	**20·3** (50)	50	20·3 ± 0·30
1944	.	.	.	.	.	.	.	.	.	.	**20·2** (5)	19·3 (8)	13	19·6 ± 0·78
1943	.	.	.	.	.	.	.	.	.	**21·3** (4)	20·9 (17)	20·2 (6)	27	20·8 ± 0·36
1942	.	.	.	.	.	.	.	.	.	19·1 (18)	18·3 (12)	18·9 (2)	32	18·8 ± 0·45
1941	.	.	.	.	.	.	.	**17·9** (5)	20·5 (4)	19·9 (16)	19·1 (10)	16·9 (3)	38	19·3 ± 0·33
1940	.	.	.	.	.	.	**17·0** (13)	18·5 (43)	18·6 (13)	18·3 (11)	19·2 (4)	.	90	18·4 ± 0·20
1939	.	.	.	.	.	**17·4** (68)	17·5 (62)	17·4 (37)	17·6 (2)	14·6 (3)	16·8 (2)	15·8 (1)	180	17·4 ± 0·14
1938	.	.	.	.	**20·0** (44)	17·3 (47)	18·6 (15)	17·9 (2)	.	12·6 (1)	.	.	109	18·5 ± 0·27
1937	.	.	.	**20·5** (26)	20·3 (19)	19·4 (6)	15·6 (2)	.	.	.	.	.	53	20·1 ± 0·31
1936	.	.	**18·2** (35)	15·8 (27)	15·8 (5)	.	19·5 (1)	.	.	.	.	.	68	17·1 ± 0·46
1935	.	**20·7** (2)	16·6 (26)	14·4 (16)	18·2 (3)	17·8 (3)	14·7 (1)	.	.	.	.	.	51	16·2 ± 0·58
1934	**19·9** (1)	17·9 (2)	14·3 (13)	14·3 (11)	16·0 (1)	16·0 (1)	.	.	.	.	.	.	29	14·9 ± 0·55
1933	16·8 (8)	17·3 (6)	15·0 (2)	14·3 (6)	.	.	.	.	.	.	.	.	22	16·1 ± 0·50
1932	15·1 (4)	15·6 (3)	.	.	.	.	.	.	.	.	.	.	7	15·3 ± 0·44
1931	.	16·0 (1)	.	8·5 (1)	.	.	.	.	.	.	.	.	2	12·3

1944	.	.	.	.	.	.	.	.	.	.	.	**23·9** (8)	8	23·9 ± 0·82
1943	.	.	.	.	.	.	.	.	.	.	**23·8** (17)	24·0 (6)	23	23·9 ± 0·49
1942	.	.	.	.	.	.	.	.	.	**22·1** (18)	24·3 (12)	23·6 (2)	32	23·0 ± 0·35
1941	.	.	.	.	.	.	.	.	**24·0** (4)	23·6 (16)	24·0 (10)	21·2 (3)	33	23·6 ± 0·33
1940	.	.	.	.	.	.	.	**22·0** (43)	22·2 (13)	22·6 (11)	22·9 (4)	.	71	22·2 ± 0·18
1939	.	.	.	.	.	.	**20·7** (53)	21·1 (37)	22·4 (2)	19·8 (3)	22·8 (2)	21·7 (1)	107	21·0 ± 0·15
1938	.	.	.	.	.	**19·1** (47)	21·3 (15)	22·1 (2)	.	18·6 (1)	.	.	65	19·7 ± 0·37
1937	.	.	.	.	**24·1** (19)	21·9 (6)	19·2 (2)	.	.	.	.	.	27	23·3 ± 0·46
1936	.	.	.	**23·2** (27)	22·6 (5)	.	23·5 (1)	.	.	.	.	.	33	23·1 ± 0·34
1935	.	.	**24·4** (3)	22·3 (16)	24·6 (3)	21·4 (3)	19·0 (1)	.	.	.	.	.	49	22·1 ± 0·34
1934	.	**22·6** (2)	20·9 (13)	20·8 (11)	19·5 (1)	20·0 (1)	.	.	.	.	.	.	28	20·9 ± 0·36
1933	**21·4** (8)	21·7 (6)	18·4 (2)	19·8 (6)	.	.	.	.	.	.	.	.	22	20·8 ± 0·34
1932	19·3 (4)	19·4 (3)	.	.	.	.	.	.	.	.	.	.	7	19·3 ± 0·26
1931	.	19·0 (1)	.	18·5 (1)	.	.	.	.	.	.	.	.	2	18·8

Four-year-old fish

1944	.	.	.	.	.	.	.	.	.	.	.	**26·9** (6)	6	26·9 ± 0·33
1943	.	.	.	.	.	.	.	.	.	.	**26·6** (12)	25·3 (2)	14	26·4 ± 0·47
1942	.	.	.	.	.	.	.	.	.	**25·5** (16)	26·3 (10)	23·7 (3)	29	25·6 ± 0·33
1941	.	.	.	.	.	.	.	.	**23·9** (13)	24·4 (11)	25·4 (4)	.	28	24·3 ± 0·30
1940	.	.	.	.	.	.	.	**22·8** (37)	24·3 (2)	23·8 (3)	24·8 (2)	23·5 (1)	45	23·0 ± 0·26
1939	.	.	.	.	.	.	**22·8** (15)	24·4 (2)	.	22·0 (1)	.	.	18	23·0 ± 0·53
1938	.	.	.	.	.	**23·7**(6)	22·1 (2)	.	.	.	.	.	8	23·3 ± 1·01
1937	.	.	.	.	**25·3** (5)	.	25·5 (1)	.	.	.	.	.	6	25·4 ± 0·79
1936	.	.	.	**25·8** (16)	24·7 (3)	23·7 (3)	.	.	.	.	.	.	23	25·2 ± 0·41
1935	.	.	**24·4** (13)	24·4 (11)	22·2 (1)	22·5 (1)	.	.	.	.	.	.	26	24·2 ± 0·32
1934	.	**24·4** (6)	20·9 (2)	22·9 (6)	.	.	.	.	.	.	.	.	14	23·2 ± 0·41
1933	**22·6** (4)	23·3 (3)	.	.	.	.	.	.	.	.	.	.	7	22·9 ± 0·30
1932	.	21·0 (1)	.	21·7 (1)	.	.	.	.	.	.	.	.	2	21·4
1931	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Five-year-old fish

1943	.	.	.	.	.	.	.	.	.	.	.	**27·0** (2)	2	27·0
1942	.	.	.	.	.	.	.	.	.	.	**27·9** (10)	25·9 (3)	13	27·4 ± 0·70
1941	.	.	.	.	.	.	.	.	.	**26·0** (11)	27·2 (4)	.	15	26·3 ± 0·33
1940	.	.	.	.	.	.	.	.	**25·5** (2)	25·7 (3)	27·0 (2)	26·4 (1)	8	26·1 ± 0·81
1939	.	.	.	.	.	.	.	**25·5** (2)	.	24·0 (1)	.	.	3	25·0
1938	.	.	.	.	.	.	**24·7** (2)	.	.	.	.	.	2	24·7
1937	.	.	.	.	.	.	26·9 (1)	.	.	.	.	.	1	26·9
1936	.	.	.	.	.	**26·8** (3)	25·4 (3)	24·0 (1)	.	.	.	.	7	25·8 ± 0·57
1935	.	.	.	.	**26·6** (11)	24·7 (1)	23·5 (1)	.	.	.	.	.	13	26·2 ± 0·43
1934	.	.	.	**22·9** (2)	25·4 (6)	.	.	.	.	.	.	.	8	24·8 ± 0·57
1933	.	.	.	.	.	.	.	.	.	.	.	.	3	25·6
1932	.	**25·6** (3)	.	.	.	.	.	.	.	.	.	.	2	23·0
1931	.	23·0 (1)	.	23·0 (1)	.	.	.	.	.	.	.	.	.	.

Six-year-old fish

1942	.	.	.	.	.	.	.	.	.	.	.	**27·2** (3)	3	27·2
1941	.	.	.	.	.	.	.	.	.	.	**28·4** (4)	.	4	28·4
1940	.	.	.	.	.	.	.	.	.	**27·2** (3)	28·3 (2)	28·9 (1)	6	27·8 ± 0·84
1939	.	.	.	.	.	.	.	.	.	25·6 (1)	.	.	1	25·6
1938	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1937	.	.	.	.	.	.	**28·0** (1)	.	.	.	.	.	1	28·0
1936	.	.	.	.	.	**27·0** (3)	26·0 (1)	.	.	.	.	.	4	26·7
1935	.	.	.	.	**26·3** (1)	24·5 (1)	.	.	.	.	.	.	2	25·4
1934	.	.	.	**27·2** (6)	.	.	.	.	.	.	.	.	6	27·2 ± 0·31
1933	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1932	.	**25·8** (1)	.	25·5 (1)	.	.	.	.	.	.	.	.	2	25·7
1931	.	.	.	.	.	.	.	.	.	.	.	.	.	.

for 53 2-year-old fish, which because they belonged to the 1937 year class were therefore living contemporaneously. The grand means are also shown graphically in Figs. 5 and 6.

The data in Table 8 provide a check on any errors that might be associated with sampling and back-calculation. The mean lengths of fish of the same age and year-class back-calculated from successive age-groups show no consistent trends, so that Lee's phenomenon seems to be absent. In some instances, however, among the fish 1 and 2 years old, it has been found that the mean lengths obtained from actual fish are greater than the corresponding ones back-calculated. This is probably due to selection by the net of larger individuals among the 1- and 2-year-old fish, but only in three cases (one among fish collected in 1937 and two among collections of 1939) has there been any significant influence on the grand mean, and as these did not affect the general trend of growth during 1937 and 1939 the cases are ignored.

(*b*) *Growth of fish of different ages*

The mean length attained for age, for fish of 1–6 years old, during the years 1932–46, is given by the grand means (for which standard errors are also given) in Table 8. In Fig. 5 these grand means together with twice the standard error of the mean, is shown for fish of 1–4 years old, the means only are shown for 5-year-old fish, the mean lengths of 6-year-olds is not figured as the data are too few. The variation in growth of the fish during 1932–46 is apparent from Table 8 and Fig. 5.

Fig. 5 shows that the mean lengths of 1-year-old fish have fairly wide variations from year to year and the values for 1937 to 1940 are, statistically, significantly higher than for any other years. Among fish of 2 years old the mean lengths for 1933–38 except for 1935 show an upward trend, and after a fall in 1939 and 1940 the mean figures rise again and are significantly above those of the earlier years, 1933–37. The mean lengths for fish of 3 years old rise steadily from 1934 to 1939, fall in 1940 and rise again to a high level, which, though not significantly higher than 1937–39, is significantly above that of the means for 1932–36. Among 4-year-old fish the mean lengths rise from 1935 to 1939, fall from 1940 to 1942 and then rise again; the levels of this last rise are, however, not significantly above those of the earlier rise of 1935–39. The mean lengths of the 5-year-olds show a general tendency to rise until 1940; then there is a fall followed by an upward trend to 1941. The mean lengths for 6-year-olds from the different years are based on too few data to be of any comparative value. The upward trend in the length attained by the 2-, 3- and 4-year-old fish during the period 1932–46 suggested by visual appreciation of Fig. 5 has no statistical significance.

(*c*) *Growth of each year-class*

The mean lengths for age already shown in Fig. 5 are plotted on a logarithmic scale in Fig. 6, but here the points are joined so that the mean growth-rate of a year-class is shown. In this figure the mean length of fry (0+), accepted as 2·5 cm. for all fish, is also given. Comparison of the curves in Fig. 6 shows that certain year-classes have throughout their existence grown faster than others; for example, the 1936 year-class has grown faster than that of 1933 and 1935, and that of 1940 faster than 1939, but when the standard errors of the mean lengths (shown in Fig. 5) are taken into account

it is apparent that, although at some period the growth of a year-class can be statistically significantly better than that of the comparable period in another year-class, there is no year-class that has *throughout its existence* grown statistically significantly faster than any other. Visual appreciation of Fig. 6 suggests that all the four year-classes 1932–35 grew more slowly than any of the 4 years 1940–43, and it was thought justifiable to combine the figures for the years 1932–35 and compare them with the figures for 1940–43. The mean lengths (in cm.) attained for each age for the grouped four years were as follows:

Years old	1	2	3	4	5	6
1932–5	7·27	15·99	21·3	24·2	25·7	26·7
1940–3	8·79	19·2	22·8	25·4	26·4	27·2

Growth in the earlier period is appreciably slower than in the later one, but the difference is only statistically significant in the 1st and 2nd years where 95% confidence limits of 0·35 and 0·62 for the 1st years and 0·50 and 0·31 for the 2nd years show these means to be highly significantly different from each other.

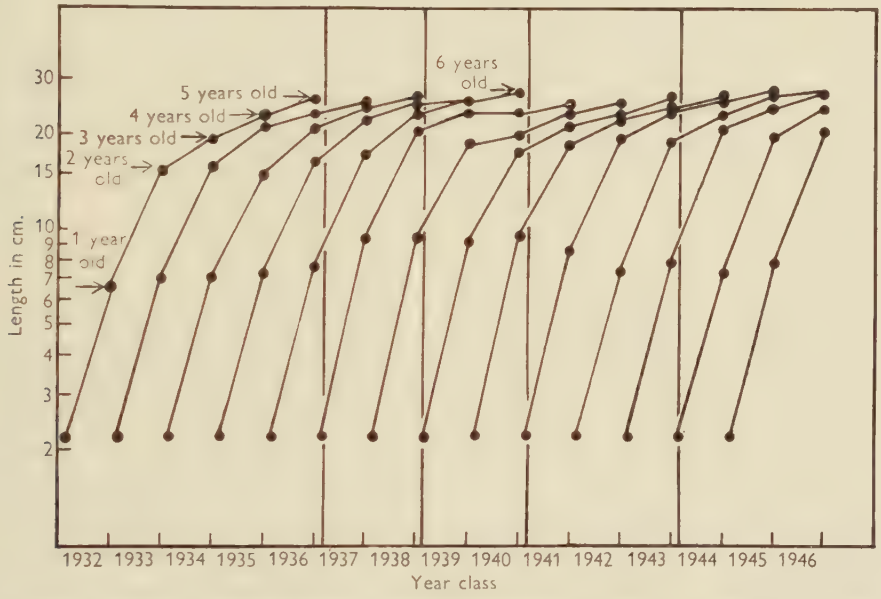

Fig. 6. Growth of each year class, 1932–45 (log scale) of trout in Three Dubs Tarn. The times of addition of bonemeal to the tarn are shown by vertical lines.

(*d*) *Specific growth-rate*

The specific growth-rate for fish during their 1st, 2nd, 3rd and 4th years of life has been calculated from the formula

$$G = \log_e Y_t - \log_e Y_0,$$

where Y_t = length attained at the end of each year and Y_0 = length at the beginning of the year; for the first year Y_0 is taken as 2·5 cm. for all fish. The specific growth is expressed as percentage per annum, and these results are shown graphically in Fig. 7. During 1932–46 the specific growth-rate during the 1st year is at a high level and also in some instances during the 2nd year of life; a much lower level characterizes the

3rd and 4th years of life. From 1937 to 1942 the rise in specific growth during the 1st year of life occurs contemporaneously with a fall in the specific growth of fish in the 2nd year, this is of interest since the fish were living under the same environmental conditions, and it appears to be a demonstration of the phenomenon of compensatory growth.

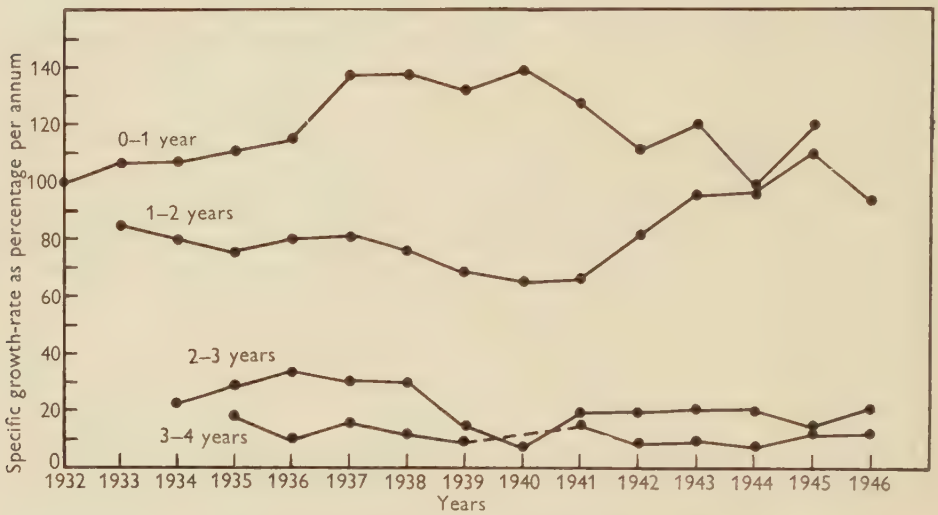

Fig. 7. Specific growth-rate of trout in Three Dubs Tarn.

(*e*) '*Condition*' *of the trout*

The relationship of length to weight has been calculated as a 'condition factor' (K) determined from the formula $K = 100W/L^3$, where W = weight in grams and L = length in centimetres, which gives a value for K of 1·0 for a trout in good condition. The values for K have been calculated for each fish, the mean K for each age (for each year's collection) is based on the sum of these individual calculations and the grand mean for each age based on all the collections, 1936–47, was obtained in the same way. The mean K for each separate year's collection was obtained by adding the means of the fish of all ages in the collection and dividing the result by the number of age-groups present, so that the effect of different numbers of fish in each age-group is eliminated. The results obtained from the different calculations are given in Table 9.

The values of K for each year's collection show some variation, but over the period 1936–47 none is markedly different from another. The 1-year-old fish have a fairly wide range of values of K, but among these smaller fish selection by the net of the fatter fish may have determined the value of K and so account for the different 'condition' in the various years. Among the 2-year-old fish there is comparatively little variation in the values for K whether or not the fish were small enough for net-selection. The values of K for 3-year-old fish show singularly little variation with the year of collection of the fish. Comparison of the mean values of K for the 4- and 5-year-old trout is of little value because they will have been affected by spent fish whose numbers and condition depend respectively on their year and date of capture, factors which varied over the period 1936–47.

The mean value of K for all the fish examined, 1·09 (calculated in the same way as the means for each separate year's collection), indicates that the trout in Three Dubs Tarn are, irrespective of age, in good condition, and the mean values of K for all fish show that, apart from the one 8-year-old fish, the condition of the trout at any age is good. In comparing the condition of the fish at different ages it must be remembered, however, that the values of K for those of 1 and possibly 2 years old may have been affected by net-selection, and those of 4 years and older by spawning of the fish.

Table 9. *Condition, given as values of* $K = 100W/L^3$, *of trout from each year's seine collection*

(Number of fish in brackets.)

Date of collection	Age of fish in years								Mean
	1	2	3	4	5	6	7	8	
26 July 1936	1·21 (6)	1·07 (1)	1·13 (6)	1·10 (2)	.	.	.	.	1·13
23 Mar. 1937	.	1·20 (4)	1·07 (10)	0·99 (1)	1·06 (3)	.	.	.	1·08
5 Apr. 1938	1·20 (28)	1·17 (17)	1·07 (19)	1·07 (6)	1·18 (1)	.	.	.	1·14
20 Mar. 1939	0·94 (3)	1·10 (26)	1·05 (27)	1·00 (16)	1·00 (11)	1·00 (6)	.	.	1·00
25 Mar. 1940	1·13 (9)	1·10 (43)	1·08 (62)	0·95 (5)	0·98 (3)	0·94 (1)	.	.	1·03
26 Mar. 1941	1·64 (1)	1·26 (73)	1·15 (47)	1·04 (6)	.	0·90 (3)	0·87 (1)	.	1·14
1 Apr. 1942	2·06 (1)	1·34 (13)	1·12 (59)	1·05 (15)	0·69 (2)	0·91 (1)	0·81 (1)	.	1·14
3 Mar. 1943	.	1·40 (5)	1·19 (43)	1·16 (37)	1·07 (2)	.	.	.	1·20
14 Mar. 1944	.	.	1·07 (4)	1·13 (13)	0·98 (2)	.	.	.	1·06
26 Apr. 1945	.	1·23 (4)	1·23 (18)	1·11 (16)	1·17 (11)	1·14 (3)	1·15 (1)	.	1·16
2 May 1946	.	1·25 (5)	1·31 (17)	1·14 (12)	1·12 (10)	1·13 (4)	1·26 (2)	.	1·20
15 May 1947	1·46 (4)	1·21 (49)	1·25 (7)	0·97 (6)	0·97 (2)	0·96 (3)	.	0·88 (1)	1·10
Mean value for all fish	1·22 (52)	1·20 (240)	1·15 (310)	1·09 (135)	1·02 (47)	1·07 (21)	1·07 (5)	0·88 (1)	1·09

DISCUSSION AND CONCLUSIONS

The difference in growth made by the different year-classes of the trout of Three Dubs Tarn during the years 1936–47 shows that among fish of the same age there may be considerable variation in the length attained. One obvious reason for such variations might be sought in differences in the population-density year by year, but a comparison of this kind is precluded as figures for absolute populations are not available. The relative size of the population of the year-classes has however been determined (Table 5), and as these data cover several years they are likely to be a fairly sound index of the comparative size of the year-classes. Growth made by the largest year-classes, 1938 and 1939, is slower than that of any other year-class. In several instances comparison of big and relatively small year-classes, such as 1938 with 1937, 1939 with 1940, and 1940 with 1941, shows that the big class has a poorer rate of growth than the small, but comparing 1943 with 1944 the larger year-class shows the better growth. When the year-classes are of equal size, as 1935 and 1936, the latter made consistently better growth than the former, but in 1941 and 1942 the same size of year-class is associated with much the same growth. On the whole, the evidence suggests that there is some association between the larger year-classes and poorer growth.

The study of the growth of trout in Three Dubs Tarn was primarily undertaken to see the effect on the fish growth of the addition of bonemeal to the tarn in 1937, 1939, 1941 and 1944 (p. 63). Comment on the variations of growth in relation to the addition of the fertilizer are based on Figs. 5 and 6. When the length attained for age

(Fig. 5) in those years (1932–36) before the addition of bonemeal is compared with that attained in the years (1937–46) after the addition, statistically significantly faster growth is found as follows: of the nine post-bonemeal 1-year-olds four had grown faster than in the five pre-bonemeal years, of the ten post-bonemeal 2-year-olds six grew faster than in the four pre-bonemeal years, of the ten post-bonemeal 3-year-olds seven grew faster than in the three pre-bonemeal years, of the ten 4-year-old post-bonemeal, five had grown faster than in the two pre-bonemeal years. There are therefore instances among all age-groups of statistically significantly faster growth being made in the post-bonemeal period, but such instances do not result in any individual year-class (Fig. 6) of this period showing faster growth throughout its life than any year-class of the pre-bonemeal period. It has been shown that the year-classes 1940–43 considered collectively had made faster growth throughout life than those of 1932–35 collectively, and in their 1st and 2nd years this difference was statistically significant. The better growth made by the post-bonemeal year-classes is suggestive, but the fact that the increase in growth-rate was significant only during the first 2 years implies that the response to the fertilizer, if such it was, was really limited to the early life of the fish.

The effect of bonemeal on the growth of the trout would be most obviously registered by the specific growth made during the year in which bonemeal was added. The data in Fig. 7 for the years 1937, 1939, 1941 and 1944 for fish of all years (0–1 etc.) show that although there were instances of higher specific growth-rate in 1937, 1939, 1941 and 1944 there was no consistent trend.

Variations in the condition of the trout in relation to bonemeal additions are deduced from comparison of the values of K for collections of fish made in 1937, 1939, 1941 and 1944 with the values for the years 1938, 1940, 1942 and 1945, years after the additions. The comparisons show that although there are instances of improved condition in bonemeal years this is not invariable.

The variations in the size of the trout when considered in relation to the bonemeal additions may be extended to a consideration of such variations and the effect of bone-meal in the fauna. Macan (1949, p. 178, Fig. 4) found that after the bonemeal additions of 1937 and 1939 the mud fauna, particularly the chironomid larvae, oligochaetes and *Pisidium*, increased about ten times, increases which were apparent in his faunistic samples of 1938, 1940 and 1941. Comparison of the size attained by the trout in these years with that attained in pre-bonemeal years shows that in 1938 fish of all ages showed statistically significantly faster growth, in 1940 the 1-year-old fish were faster, the others slower, and in 1941 only the 2-year-olds grew faster. From these results there is some suggestion of improved growth being associated with the increase of food supply which followed 'fertilization', but such association is not invariable.

Thus, although after the addition of bonemeal there were instances of statistically significantly improved growth, since these showed no consistent trend and no better growth of any year-class, the fertilizer cannot be regarded as a major factor affecting the trout-growth.

Of the remaining possible causes of variation in the growth-rate of the trout, the weather conditions, temperature, amount of water in the beck and tarn, etc. little is known. The spawning beck is dry at some time during the year and the time of

drought no doubt influences the time of descent of the fry. In some summers the water-level of Three Dubs Tarn was lowered, the extent and duration of the fall in level depending on the weather and the demand for a head of water. It is thought that in most years the fall was such that little of the tarn bottom was exposed so that the desiccation of the fauna would be negligible. In 1940, however, the tarn was lowered by 2 ft. 9 in. for some weeks, and this, if it resulted in the depletion of the fauna, may be associated with the size of the 1940 trout, the mean lengths of which are all below those of the previous and subsequent years.

In spite of the variations in the growth of the Three Dubs Tarn trout, over a period of years there is a general pattern of growth which characterizes the growth of the fish in this tarn. This has already been described (p. 73) and figured (Fig. 4), and it is of interest to note that the pattern is essentially the same as that for Three Dubs trout in the years before any bonemeal was added (Swynnerton & Worthington 1939). The addition of the bonemeal was an attempt to 'maintain the good growth after the second and third year of life' (Swynnerton & Worthington 1939). That this has to some extent been achieved is suggested by those increases in length of 3- and 4-year-old fish noted on pp. 77–8, but as such increases were statistically significant in one or two instances only and the actual amount made was never great, the growth of the trout after the 2nd year of life still remains poor compared with that of the earlier years. Some reasons which may account for the pattern of growth of Three Dubs trout may be suggested if a comparison be made of this growth with that made by the trout in Windermere and Yew Tree Tarn (Fig. 4 and Table 7), two waters which are essentially of the same type as Three Dubs Tarn in that they are base-deficient and poor in electrolytes with a low pH-value. Windermere is, however, far greater in size ($5\frac{1}{2}$ sq.miles; 17 sq.km.) than Three Dubs; Yew Tree Tarn has the same area as Three Dubs Tarn.

Fig. 4 shows that the trout of Three Dubs Tarn are appreciably greater in length at the end of their 1st and 2nd years than those of Windermere, that by the 3rd year the trout of the two waters are the same length, and that subsequently Three Dubs fish are much less in length than trout of the same age from Windermere. It also shows that the trout of the tarn are always longer than those of the same age from Yew Tree Tarn. The specific growth-rate of the fish for the three localities (Table 7) shows that Three Dubs trout had attained a larger size in their 1st year (0–1) than trout from the other two waters, and this resulted in their being greater in length at 1 and 2 years old than were Windermere fish of the same age and for their having a greater length at any age than the Yew Tree Tarn trout.

One of the reasons for these differences in growth of trout in the three waters may be found in the food supply, either in quantity or quality or both. There is no information on the amount and quality of the food supply in Yew Tree Tarn, but Swynnerton & Worthington (1939) remark that as the spawning facilities for trout in this water are excellent the 'tarn receives a great number of young fish each year and is permanently over-stocked. The effect of all these fish must be to keep the food supply at a very low ebb and this supply is probably shared by minnows which abound.' From these remarks it may be deduced that one cause of the poor growth throughout life that characterizes the trout of Yew Tree Tarn is scarcity of food. Attention has already

been drawn to the fact that, in Three Dubs Tarn, the mud fauna is more abundant than that of the weeds and that, relative to the supplies of these animals, the weed organisms are more heavily grazed by the trout, and it has also been noted that both large and small trout feed to much the same extent on weed-dwellers (p. 69). Now, apart from *Sialis*, the weed organisms are larger than those of the mud so that if it be assumed that big trout will need more of the larger foods than the small trout then it follows that, because of the poverty of the weed fauna and its being cropped by fish of all sizes, the requirements of the big trout cannot be met, and in consequence growth in the later years is slow. Although the mud fauna presents an abundant supply of food the individuals are mostly small and often inaccessible which limits their value as food for the trout. The small trout do feed more heavily upon the mud-living organisms than the larger fish (Table 3), and this together with the amount of larger foods (weed-dwellers) that they also eat would seem to provide an adequate diet, which is reflected in the good growth made by the fish in the first two years of life. The decline in growth after the third year so characteristic of Three Dubs trout is not found among the Windermere fish. In Windermere the larger food organisms, especially the gastropods of the littoral zone, are considerably better represented in species (Macan, 1950) and numbers (Humphries, 1936) than in the tarn; in Windermere too there are forage fish, such as minnows (*Phoxinus phoxinus* L.) and perch, (*Perca fluviatilis* L.) which are absent from the tarn. Comparatively the trout of Windermere suffer from no shortage of larger food organisms so that in quality and quantity the food supply is conducive of good growth in the later years. In their 1st and 2nd years, however, the growth of the Windermere trout is appreciably slower than that of the tarn ones, years which are spent in the inflowing streams of Windermere where the food supply being shared by bullheads (*Cottus gobio* L.), minnows, eels (*Anguilla anguilla* L.), and indigenous trout is likely to be less abundant than that for the young Three Dubs trout, which leaving the beck early in their 1st year feed in the tarn where there are no other species of fish as competitors.

Of space as a factor determining the size of fish Alm (1939) writes that it is 'well known that trout are usually bigger in large than in small lakes'. He shows from his own experimental ponds, where food was abundant, that growth of the brown trout was better in those where there were fewer trout per unit area. Allen (1938) estimated that in the littoral zone of Windermere, which if limited by the 2 m. contour consists of 12·8 sq.km. (Mortimer & Worthington 1942) there were 12,000 trout, which would mean each having 1000 sq.m. If 300 trout are allotted to Three Dubs Tarn (16,000 sq.m.) each has 53 sq.m., an area per fish roughly one-twentieth that in Windermere. The spatial factor during the first 2 years of growth of Windermere fish would be different as the trout are then in the river. Thus the lake fish may make poorer growth during early life than the tarn trout because the latter have more space per fish at this time than the young trout in the river, but the subsequent growth of the lake and tarn fish would reflect the great differences in the space available to each fish. Recently, the effect of food and space on the growth of trout was shown by fish taken from a tarn near to Three Dubs, which had been drained and dried out in 1949 and when presumably fishless was refilled. In July 1951 four brown trout and five *Salvelinus fontinalis* were taken from it; two of the brown trout were 37 cm. (700 g.)

and 39·5 cm. (775 g.); the age from the scales was 2+ years so that doubtless these fish were fry when the tarn was drained. In the tarn there are great numbers of introduced *Vivipara*, so that the nine fish would have a good supply of large food organisms and much space per fish, factors which no doubt accounted for the rapid growth of the brown trout.

Mention must be made of any difference in the age at which sexual maturity is attained by Windermere and Three Dubs trout, for growth is slowed down by reproduction. The age at which Windermere trout become sexually mature is not given by Allen (1938), but it is most likely that it occurs at the end of the 4th year. Since in Three Dubs Tarn the majority of trout spawn for the first time at this age also, maturity does not explain the marked difference between the growth of Windermere and Three Dubs trout in their later years.

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SUMMARY

1. A biological survey of Three Dubs Tarn, in the English Lake District, has been made. The flora and invertebrate fauna have been described by Macan (1949), the food, age and growth of the brown trout (*Salmo trutta* L.), the only fish present, are described from material collected from 1936 to 1947.

2. The tarn has an area of 4 acres, and is 700 ft. above sea-level. Its water is poor in electrolytes, and has a low calcium content. Bonemeal was added in 1937, 1939, 1941 and 1944.

3. The trout range in length from 7·5 to 28·7 cm., the majority being 21·8 cm. and weighing 126 g. In age they range from 1 to 8 years; they enter the tarn, from the beck, in their 1st year. The mean survival rate for fish of all ages is 39%.

4. From March to September the food consists mainly of the larvae, nymphs and pupae of aquatic insects; *Pisidium* and surface terrestrial organisms are frequently eaten. Comparison of the food and fauna shows that in general the fish eat what is available and abundant, but there is evidence of preference and avoidance. The trout feed as frequently on weed-living organisms as on mud-living ones, although the weed fauna is poorer than that of the mud.

5. The general growth-pattern, based on all data 1936–47, shows that growth was fastest during the first 2 years of life, slower in the 3rd year and declined steadily thereafter.

6. With the different years (1932–46) there was considerable variation in the length attained by an age-group, but no one year-class had grown better throughout its existence than any other. The values of K indicate that the 'condition' of the trout, of all ages, is good; this is true of periods both before and after addition of bonemeal.

7. The effect of bonemeal on growth cannot be isolated from that of other factors, although instances of significantly increased growth-rate coincident with the bonemeal additions were found; but such improvement was not sustained.

8. Comparison of the growth of trout in Three Dubs Tarn with that in two waters of similar chemical character, Windermere and Yew Tree Tarn, suggest that differences in food and spatial conditions account for the differences in size attained by the fish.

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THE SMALL ARTHROPODS OF A *MOLINIA* FEN AT COTHILL

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(With Plate 2 and 2 Figures in the Text)

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INTRODUCTION

This paper describes a 1-year census of the small arthropods of 5·4 acres of fen at Cothill, Berkshire, which is 5 miles south-west of Oxford and marked on the Ordnance Survey maps as 'Parcel 6' (Nat. Grid Ref. 41/463998). The area in question is described more fully in the next section; it was chosen for study because it appeared to have a rather uniform vegetation, a shallow inhabitable soil and therefore might be expected to have a relatively simple soil fauna and also because some work had been done on the botany of the larger plants and the peat by Prof. A. R. Clapham of Sheffield University and on the soil fungi by Mr J. Harper of Oxford University Botany Department.

Factors which were not anticipated when the study was commenced were that the area has subsequently been grazed by cattle and that the fen was fired by local people, possibly in order to drive rabbits from the *Molinia* tussocks, once while the study was in progress and at least twice between that time and 1951. An investigation of the effect of the burning was not one of the primary objects of the present study, but it has been possible to extract some information on this and also continue with the investigation as originally planned because the burning did not cover the whole area.

The original intention was to combine three investigations. First, a census of the small arthropods (mainly the mites and Collembola); secondly, a physiological study of the metabolic rates of the more important animals present; and thirdly, a microclimatic study of the upper layers of the soil. Thus the total metabolic activity of the populations in the field could have been estimated and comparisons made between the effects of each species at different seasons and in different areas (see Macfadyen 1948). Owing to a number of factors, of which interference by man and by cattle with the area and with apparatus, and difficulties with the microclimatic measurements were the chief, these further objectives were postponed and a new census in the greater security of Wytham Woods, Berkshire, has since been carried out in conjunction with Dr C. Overgaard Nielsen.

In the course of the investigation a considerable number of animals other than mites and Collembola was encountered; most of these have now been identified and a list is included in Appendix I for the benefit of future workers.

DESCRIPTION OF THE AREA

The area in question occupies 5·4 acres and might be described as an advanced fen resting on at least 14 ft. of peat (Clapham, personal communication). It is almost level and surrounded on two sides by rapidly flowing streams containing slightly calcareous water. The fen has not been observed to flood. The ground surface is made uneven by tussocks of *Molinia caerulea* (Pl. 2*A*) which probably undergo a prolonged cycle of elevation and degeneration; these are interspersed with lower tussocks of *Deschampsia caespitosa* (Pl. 2*B*), and in places with *Arrhenatherum avenaceum*. Lower channels between the tussocks are mainly filled with *Juncus subnodulosus* with some tussocks of *J. reflexus*, although a considerable part of this area, which on rare occasions was slightly flooded with rain, is covered with flattened stems of *J. subnodulosus* or *Molinia*, or has either bare earth or a thin moss covering. A considerable amount of *Molinia* grows between the tussocks at the same level as the *Juncus subnodulosus*. Among other plants which are widespread are a *Poa*, a *Festuca*, *Ulmaria*, *Carex*, *Prunella vulgaris*, *Cnicus palustris* and various mosses. The relative proportions of the area covered by the main plants varies somewhat over the fen but measurements from a number of transects indicate that *Molinia* tussocks occupy about 10% of the area, *Juncus subnodulosus* about 7% and *Deschampsia* about 5%; of the remainder *Molinia* growing not in tussocks covers at least 50%.

METHODS

One subject on which opinion seems to be divided is whether the population figures should be expressed in numbers per unit area of the soil surface or per unit volume of the medium in which they live. Many workers (cf. Strenzke 1949*b*; Weis-Fogh 1948) are agreed that an ideal basis would be the surface area of the pore spaces in the soil available to each animal, but since no method of measuring this has been devised it cannot yet be employed in practical studies. Practice in the past has varied, and for this reason alone it is most desirable that sufficient data should always be published to allow conversion from one basis to the other. The Danish authors (Bornebusch 1930; Hammer 1944; Tuxen 1944; Overgaard 1949; Weis-Fogh 1948), as well as Ford (1935, 1937, 1938) and Salt, Hollick, Raw & Brian (1948) in England, and

Photo: D. A. Kempson

A. A tussock of *Molinia caerulea* (L.) Moench.

Photo: D. A. Kempson

B. A tussock of *Deschampsia caespitosa* (L.) Beauv.

[Scales in feet with 3 in. divisions.]

Strenzke (1949*a*) in Germany, have all used area as a basis, while Agrell (1941), Forsslund (1945), Van Der Drift (1950), and Glasgow (1939), have all used volume. Tuxen argues the case for an area basis on p. 168 of his paper, expressing views which to some extent coincide with those given below. Strenzke (1949*a*) takes the same view and adopts a very good method; he samples on an area basis and then subdivides the samples into their natural vertical strata. Forsslund and Van Der Drift, when investigating forest litter and soil, claimed that volume was a more accurate and convenient measure than area, but the latter worked out conversion factors so that volumes could be converted to areas. Glasgow argued that for animals living 'in the bottom of vegetation the density must be calculated on a basis which makes allowance for the density of the vegetation'; his object therefore seems to be to introduce a factor which will make all populations more equal by reducing the variation due to plant density. I feel that area is a more suitable basis for expressing population density for the following reasons:

(1) The primary energy cycle only has significance on an area basis. We know, for instance, that an average of about 336 calories of the sun's energy reach each square centimetre of the *surface* of the earth each day; that a proportion of this energy is transferred to food substances by the plants, which are themselves growing in a very thin layer at the interface between the earth and the atmosphere; and that this energy-rich food is the 'power supply' for all the living organisms which occur in association with this interface. The importance and activity of the populations themselves can only be assessed in relation to the production of plant matter so that productivity studies are only possible on an area basis.

(2) It has been found by all investigators that the density of the populations of the microfauna and flora is greatest at or just under the interface between the soil and the litter and that the population density falls off extremely rapidly in both directions even in a vertical distance of a few centimetres. If, therefore, the population is expressed in terms of volumes of material and if larger samples of a given layer are collected in places where that layer is more thinly spread, varying proportions of the richer layers will be included in a given volume of medium. The comparison of samples taken in, say, litter layers of varying thickness will then give a misleading impression that the population is denser in places where the litter is shallower.

It was for these reasons that area was adopted as the standard basis for comparison in the present study; all sampling units were 10 sq.cm. in area. Normally a depth of only 5 cm. was used, but three sets of sampling units extended to 15 cm. in three stages so that the distribution of the fauna at greater depths could be estimated. As will be shown, not more than 33% of the whole fauna occurred below 5 cm. and this figure was probably only reached for a short period of the year. Conversion of the figures to volumes of soil can be easily carried out because each sampling unit contained 50 c.c. of material.

The fen is not an area of uniform vegetation, and preliminary samples showed that the fauna varied much between the main plant types. It was therefore decided that random sampling would be wasteful of effort and that the sampling units taken should be divided evenly between the three main plant types. It is desirable in a study of this sort to know whether the distribution of the animals is uniform over the area

under study; the simplest method of learning this is to take the sampling units in adjacent pairs so that differences due to sampling position over the area may be compared with differences between pairs. The maximum number of sampling units, it was decided, which could conveniently be extracted and sorted was thirty per month, and five pairs of sampling units were therefore allotted to each of the three plant types in each month. The position for each of the pairs was determined by throwing a stick and taking the pair of units in the nearest example of each plant type to the position where the stick landed. This method was used because the complete vegetation mapping, which a truly random method of sampling would entail, was deemed impracticable.

The analysis of variance of the thirty counts made in each month therefore involved the following subdivision of degrees of freedom:

	D.F.
Plant types (3)	2
Positions (5)	4
Pairs (15)	15
Interaction	8
Total (30 sampling units)	29

The 'interaction' term measures whether the difference between plant types is consistent in the different sampling positions.

It will be appreciated that the 'routine' sampling units were not taken at random, but were approximately so within each plant type. It was considered that there were considerable advantages to be gained by the analysis of the causes of variation due to the main factors (plant types and positions) in addition to those due to months and to species. For this purpose the analysis of variance technique (Fisher 1938–42; Snedecor 1937–46) is available. Examples of its use are given in Table 3 (p. 95).

At the same time it is not possible from the 'routine' sampling units to determine a 'mean density' for the area as a whole, and this is a distinct disadvantage when making rough comparisons between different studies. It is doubtful whether much meaning can be attached to a 'mean density' in an area of interspersed vegetation types if only because the density of the different types varies over the area as a whole and because marginal areas may differ in their fauna as much as the main plant types. However, for comparative purposes, two series of thirty sampling units distributed at random were taken along a transect line traversing the fen and containing a high proportion of the intermediate plant types, and the results are compared for the same months with the routine sampling units in Table 1. It will be seen that the *Molinia* and *Deschampsia* tussock faunas were considerably more dense than the random sampling units but that the *Juncus subnodulosus* fauna was less so.

In addition to the 450 sampling units just accounted for, further sampling units were taken in conjunction with the main series designed to determine the distribution of the fauna in depth. The main sampling was repeated at twice and three times the depth and this was carried out on three occasions (October 1949 and February and May 1950); this involved 180 extra units. Further units were also used to carry out various tests of extraction methods.

As a result of these samples data were obtained on the variations in the numbers of animals with *time*, with *depth*, with *plant types*, and with *horizontal distribution* over

the fen. The litter layer was not well marked in the rather impoverished area under investigation, and it was therefore decided not to attempt separate sampling of the litter and soil layers as, for instance, was done by Strenzke (1949*a*). Every sampling unit therefore includes both the litter and the soil under the circle of 10 sq.cm. The sampling units were taken by first cutting any erect plant stems and leaves with scissors to within 0·5 cm. of the litter surface and then removing these. Samples were taken by means of stainless steel tubes which contain a gauze at the upper end and are sharpened at the lower end. Each sample of soil is carried to the laboratory in its individual tube and inserted in a Tullgren funnel type-extraction apparatus, the tubes being inverted so that the animals living in the litter and unable to burrow do not have to do so in order to reach the funnels. Full details of the extraction apparatus which is designed to produce steep temperature and humidity gradients in the soil mass, are given in a separate paper (Macfadyen, in prep.). Although the absolute efficiency of the method cannot at present be assessed it is certainly higher for mites and Collembola than that of most other extraction methods now in use. The figures for other groups are not claimed to be quantitative.

Table 1. *Numbers of animals in routine, as compared with random sampling units*

(Each figure represents individuals per 10 sq.cm. and is based on ten sampling units (plant types) or thirty sampling units (random). Approximate proportions of the three plant types are *Molinia* : *Deschampsia* : *Juncus* :: 10 : 5 : 7.)

	March				May			
	Molinia	*Deschampsia*	*Juncus*	Random	*Molinia*	*Deschampsia*	*Juncus*	Random
Oribatei	124·6	100·8	10·3	24·0	160·7	73·9	14·4	28·4
Parasitiformes	12·8	5·9	2·0	3·6	8·7	17·3	3·9	6·2
Eupodidae	1·3	1·8	0·5	2·7	0·3	0·5	0·3	2·5
Collembola	20·2	19·6	5·0	8·0	21·9	14·4	4·4	13·0

The species list of micro-arthropods is given in Appendix I; in the quantitative parts of this paper, however, certain species (those marked with a dagger) are omitted from the tables because their contribution to the fauna is believed to be relatively unimportant (never more than 5% of the fauna). In order to discover the main trends in the populations the eight dominant Collembola, the twenty dominant Oribatei, and four Parasitids must be added together separately in these three groups, because there can be no meaning in adding together members of groups so diverse in their biology and size-range. Further, within each group there seems to be little point in adding one *Oppia bicarinata*, say, to one *Euzetes aterrimus* expressing the sum as 'two Oribatei' because the respective weights of these two species are of the order of 0·005 and 0·25 mg. The weighting of abundance figures by means of estimates of weight or biomass of each species, however approximate, is therefore felt to be preferable to adding together numbers of different species. Approximate biomass figures have therefore been calculated for each species by the following method:

(1) The length, breadth and depth of a number of representative adult animals were measured and multiplied together to give a volume in cubic microns.

(2) The weight of about twenty specimens of certain large and abundant species in the groups Poduromorpha, Oribatei (*Euzetes*, *Scheloribates laevigatus*, *Nanhermannia*) and Parasitoidea (*Seiodes* and *Macrocheles*), were obtained directly on an

analytical balance. A conversion factor was obtained for each species and applied to other animals as they most nearly resemble the above species in shape. The volumes were then converted into weights by multiplication by the conversion factors. The values obtained are believed sufficiently accurate for the present purpose, which demands a knowledge only of orders of magnitude.

RESULTS

The list of species given in Appendix I contains all those which have been collected. The most outstanding feature of the locality as regards the larger animals was the very low earthworm population (about one to five per square metre as determined by the potassium permanganate method and certainly low even allowing for the known imperfections of this method) and a rather high population of woodlice. It has been suggested (Franz 1943) that woodlice may to some extent replace earthworms in carrying out the primary breakdown of plant material and its mechanical incorporation in the soil, although there seems to be little precise knowledge on the subject. The extraction apparatus employed was not designed to extract the larger animals from the soil, nor forms such as dipterous larvae and Nematoda, and it is certain that a much richer fauna would have been found had the proper methods been employed. The majority of the aphids found were obtained from the soil by chemical repellants which were being tested for mites and Collembola and were not very effective for these forms.

In the following sections the effects of major environmental factors on the total numbers and biomass are considered first and then the effects on the faunistic composition and those species which do not seem to follow the general trends. It should be remembered that the generalizations about biomass apply only to the more abundant thirty-two selected species.

(*a*) *The influence of macroscopic plants on the fauna*

The most characteristic difference between the contents of the sampling units taken in this investigation is that associated with the three plant types: *Molinia caerulea*, *Deschampsia caespitosa* and *Juncus subnodulosus*. This is shown by Fig. 1 which shows the influence of plant types and season on the numbers and biomass of the Collembola and Oribatei respectively. The diagrams are based on the figures in Appendix II. The *Molinia* sampling units nearly always have more animals and a greater weight of animals than the *Juncus subnodulosus* and than the *Deschampsia*, and the differences have been shown to have statistical significance on a large number of occasions. This applies not only to the whole groups but also to most of the single species (see the analyses of variance in the next section). These very marked quantitative differences are not, however, matched by differences in the proportions of the different species which occur. No single mite or collembolan is restricted to one plant type. The most narrowly confined of all is probably *Hypocthoniella* which was found in the *Juncus subnodulosus* sampling units only twice. Whereas from the point of view of population size both single species and whole groups show marked differences between the plant types, the faunistic composition varies little. A few exceptions can be detected from comparisons of ratios in different plant types (Table 2). Thus the ratio

throughout the year of the population sizes in *Molinia*, *Deschampsia* and *Juncus subnodulosus* respectively is about 3:3:1 for Collembola (the high proportion for *Deschampsia* being mainly due to *Folsomia quadrioculata*) and 9:6:1 for Oribatei. It will be seen that the members of the group marked '*a*' show a preference for *Juncus subnodulosus* and those marked '*b*' have exceptionally high values in *Deschampsia*. (The figures are the total biomass for the 13 months in each case.) The members of the first group include among the mites, the very large species, some of which are

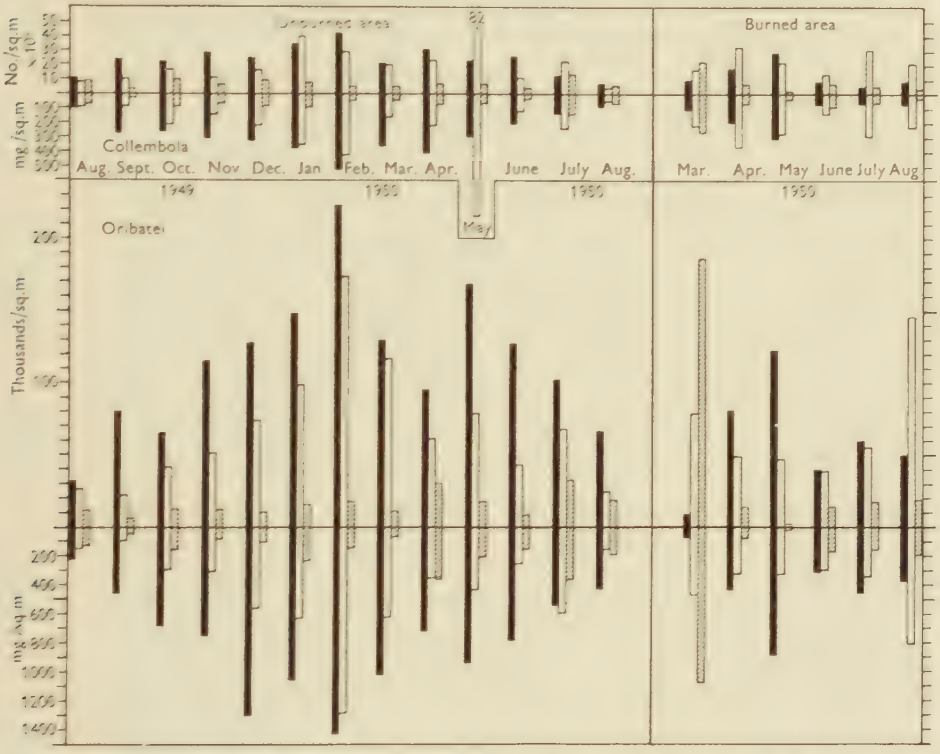

Fig. 1. Numbers and biomass of Collembola and Oribatei on Cothill fen analysed by plant types and months. The upwardly directed histograms represent numbers, those pointing downward represent biomass. In each monthly group of three histograms, the first (black) refers to *Molinia*, the second (clear) to *Deschampsia* and the third (dotted) to *Juncus* areas. After February 1950 the histograms in the first part of the diagram refer to the unburned area, while those in the right-hand block refer to the burned area. All figures up to February are the means of ten sampling units, from March onward of five sampling units.

associated with mosses and all of which are believed to be surface-dwelling forms. (Unpublished results from pitfall traps.) The fact that *Folsomia quadrioculata* is abundant in *Deschampsia* has some influence on the picture for the Collembola as a whole, since this species is certainly the most abundant and also contributes most to the biomass of Collembola. *Folsomia quadrioculata* and *Neelus* (*Megalothorax*) *minimus* are generally agreed to be surface-living forms (cf. Schaller 1949, 1950), while *Tullbergia krausbaueri* and *Onychiurus armatus* are both truly subterranean (see Schaller 1949, 1950; and also Glasgow 1939). The latter may well be poorly represented in the tussock fauna because the normal 5 cm. deep sampling units do not

extend to the deeper soil layers where they live, owing to the thicker upper layers in the tussocks. This suggestion is borne out by the figures from the May depth-sampling units (see p. 98) which indicate that *Tullbergia krausbaueri* is deeper living than *T. denisi*. Unfortunately, the distinction between this pair of species had not been learned at the time of the first two depth samples.

Table 2. *The ratios of occurrences in the three plant types of the main species of mites and Collembola*

(Figures in heavy type show marked departures from normal. Species marked *a* show a preference for *Juncus*, those marked *b* for *Deschampsia*.)

		Total numbers collected in 12 months			Ratios (*Molinia* 100)	
		Molinia	*Deschampsia*	*Juncus*	*Deschampsia*	*Juncus*
Onychurus armatus	*a*	33	8	2	24	6
O. furcifer	—	90	27	11	30	12
Tullbergia denisi	—	84	39	13	46	16
T. krausbaueri	*a*	30	11	39	37	**130**
Friesia mirabilis	—	630	494	163	78	26
Folsomia 4-oculata	*b*	1180	1815	245	**154**	21
Isotoma notabilis	*b*	139	163	140	**117**	**101**
Neelus minimus	*a*	215	46	123	21	**57**
Total Collembola		2401	2603	736	108	31
Notaspis coleoptratus	*b*	255	273	64	**107**	25
Oribatula tibialis	—	147	108	22	73	15
Scheloribates latipes	—	431	107	16	25	4
S. laevigatus	—	385	347	107	90	28
Minuthozetes semirufus	—	2289	1333	200	58	9
Ceratozetes mediocris	*b*	408	418	7	**102**	2
Euzetes aterrimus	*a*	106	25	26	24	**25**
Spherozetes orbicularis	—	363	90	30	25	8
Nanhermannia elegantula	—	980	698	96	71	10
N. elegantula nymphs	—	1568	1082	162	69	10
Malaconothrus globiger	—	809	212	33	26	4
Hypocthoniella pallidula	—	753	133	5	17	1
Cepheus dentatus	*a*	82	28	30	34	**37**
Tectocepheus velatus	*a*	90	9	20	10	**22**
Oribella castanea	*b*	9	27	2	**300**	22
Oppia neerlandica	*b*	979	1198	68	**122**	7
O. bicarinata	—	1072	618	81	58	8
Phthiracarus ligneus	*a*	76	53	80	70	**105**
Hoploderma striculum	*a*	160	84	112	53	**70**
Total Oribatei		10962	6843	1171	59	13
Parasitiformes	—	74	66	31	89	42
Trombidiformes	—	35	14	11	40	31
Tyroglyphids	*b*	5	8	4	**160**	80

(*b*) *Horizontal distribution of the fauna*

Since the sampling units were always paired it is possible to determine whether the population over the fen as a whole varies to any considerable extent as compared with the variation between the pairs. Analyses of variance have been performed on the figures for a selection from the most abundant species and the sums of squares, which measure the variation due to the differences between pairs, localities and plant types are given in Table 3. It will be seen that in a great many cases the figures are not

significantly larger for 'positions' than for pairs. This is perhaps a rather surprising result since it implies that the chances are no higher of obtaining two figures the same in adjacent sampling units than in units widely separated in different positions on the fen provided that the same plant type is sampled in each case. *Minuthozetes semirufus* and *Oppia neerlandica* provide examples of this very uniform type of distribution and

Table 3. *Analysis of variance of selected species with respect to plants, positions and pairs*

		Mean square variation due to				Mean per sampling unit	Ratios		
		Plants	Positions	Inter-action	Pairs		Pairs s^2:mean	Pairs s:mean	Positions s:mean
Degrees of freedom		... 2	4	8	15				
Minuthozetes semirufus	Aug.	141·7**	49·8	11·8	42·4	5·9	7·2	1·1	1·2
	Sept.	307·3**	66·4	52·0	31·2	5·5	5·7	1·0	1·5
	Oct.	246·9**	13·9	55·6*	17·3	6·5	2·7	0·6	0·6
	Dec.	1869·8**	524·9	391·4	265·0	15·1	17·5	1·1	1·5
	April	30·9*	13·2	8·3	11·7	3·3	3·6	1·0	1·1
	July	257·0*	208·6*	78·6	57·9	8·5	6·8	0·9	1·7
Oppia neerlandica	Aug.	8·4*	6·3	3·3	3·3	1·7	1·9	1·1	1·5
	Sept.	172·0**	24·9	27·3	24·1	3·5	7·1	1·4	1·4
	Oct.	109·9**	107·8*	29·9	27·6	4·2	6·6	1·3	2·5
	Dec.	166·8*	108·5	70·8	41·3	5·3	7·8	1·2	2·0
	April	180·2**	135·4**	50·6	20·2	5·3	3·8	0·9	2·0
	July	76·8**	9·8	29·3	14·4	3·7	3·9	1·0	0·9
Folsomia quadrioculata	Aug.	11·3	14·8*	9·1	6·8	2·6	2·6	1·0	1·5
	Sept.	252·1**	123·1	101·2	31·5	4·8	6·6	1·2	2·3
	Nov.	41·8*	26·2**	21·6**	15·4	3·7	4·2	1·1	1·4
	Jan.	182·8**	156·7*	86·6*	5·9	7·1	0·8	0·3	1·8
	June	107·7**	35·8	27·2	6·8	6·8	1·0	0·4	0·9
	July	565·9**	81·7*	90·0	40·9	9·0	4·5	0·7	1·0
Nanhermannia elegantula	Aug.	13·9*	14·7*	2·8	2·4	1·0	1·3	0·8	2·0
	Sept.	1189·6**	1460·9**	1500·9**	35·1	10·2	3·4	0·6	3·8
	Nov.	633·8**	526·0**	580·9**	49·4	9·2	5·4	0·8	2·5
	Jan.	464·1**	62·2*	134·9**	16·4	9·2	1·8	0·4	0·9
	June	1683·3**	760·4**	540·5**	51·4	13·1	3·9	0·6	2·1
	Aug.	1402·6**	1166·9**	1605·6**	29·5	17·5	1·7	0·3	2·0
Scheloribates latipes	Jan.	88·7	7·2*	24·4	13·8	5·0	2·8	0·7	0·5
	April	5·8	5·3*	2·0*	1·6	1·6	1·0	0·8	1·4
Malaconothrus globiger	July	169·8	139·8*	113·1*	40·2	6·9	5·8	0·9	1·7

* 5% significance level. ** 1% significance level.

are typical of the majority of other species. On the other hand, *Folsomia quadrioculata* and *Nanhermannia elegantula* show a more clumped distribution, indicating presumably that they are confined more to certain parts of the fen; it is not possible to say whether these areas of higher density are close together or consistent owing to the method of taking the sampling units. The more irregular distribution of *Folsomia quadrioculata* must be at least partly due to the large numbers of young found in certain samples, especially in the spring; it will be noted that the high figures occur in January and April and not at other seasons. Unfortunately no distinction was made between different size groups of Collembola when counting these samples; a defect which has been remedied in later work. *Nanhermannia elegantula* has a greater preference for the deeper layers of the soil than the other Oribatei and possibly its optimum region is near the 5 cm. level, to which the sampling units were taken. In this case a more

variable distribution with localities, dependent on a number of minor factors, could be expected.

It will be seen from a comparison of the mean squares in Table 3 that the typical species, as illustrated by *Oppia neerlandica* and *Minuthozetes semirufus*, show little evidence of a patchy distribution on a large scale.

When the occurrences of individuals are distributed at random over an area, the mean numbers found in a set of sampling units tend to be equal to the variance of these numbers in all the units, and the type of distribution obtained is known as a 'Poisson distribution'. When the variance (s^2) is greater than the mean, the distribution is no longer random but is more irregular or 'patchy' than would occur if the distribution were governed purely by the laws of chance. The ratio, in the above sampling units, of the variance for pairs to the grand mean thus gives a measure of the patchiness of distribution in the adjacent sampling units, and this ratio is given in

Table 4. *Depth-distribution of Collembola and Oribatei*

(Figures are percentages referred in each case to the population of the 0–5 cm. layer as 100; upper figures by numbers, lower (in black) by weights.)

	Molinia		*Deschampsia*		*Juncus*	
	5–10 cm.	10–15 cm.	5–10 cm.	10–15 cm.	5–10 cm.	10–15 cm.
October						
Collembola	19·6	10·4	3·1	5·2	20·0	15·9
	10·8	**8·1**	**1·6**	**6·7**	**22·0**	**2·8**
Oribatei	4·7	2·1	1·9	1·2	7·9	1·3
	2·9	**1·5**	**1·9**	**1·1**	**8·7**	**0·4**
February						
Collembola	85·3	22·5	60·1	17·8	24·3	0
	48·5	**7·6**	**47·0**	**10·8**	**20·1**	**0**
Oribatei	66·8	12·7	18·6	5·4	13·5	0
	52·3	**9·2**	**15·7**	**6·0**	**14·5**	**0**
May						
Collembola	23·4	1·8	6·4	4·0	61·9	0
	11·5	**1·7**	**6·5**	**2·1**	**47·1**	**0**
Oribatei	20·7	5·2	2·6	1·9	10·9	3·3
	28·2	**3·2**	**2·9**	**2·0**	**1·9**	**0·4**

the eighth column of Table 3. It will be seen that in nearly all cases the ratio is greater than one, indicating some aggregation of the individuals of each species. In fact the ratio of the standard deviation (s) to the mean (ninth column) is much more nearly equal to unity. This conclusion has been checked by estimating the variance from the range divided by 3·1 (see Snedecor 1946, p. 98) and dividing it by the mean in a wide range of instances.

There is no contradiction between the statements made in these last paragraphs (that there is little evidence of large-scale patchiness, but that the pairs indicate patchy distribution) because the distribution on the ground within a plant type may well be a patchy one while the patches themselves are on a small enough scale for the differences between the sampling positions to remain unaffected. It is true, however, that the estimates of the means and variances given in the tables will be to some extent inaccurate owing to their being based on a material which is not randomly distributed. The ideal method for dealing with such material would appear to be that of Thomas (1949) and of Barnes & Stanbury (1951) which involve taking very many small

samples and fitting the results to a double Poisson distribution; these methods have not yet been applied to animal populations as far as the author is aware.

(c) *Vertical distribution of the fauna*

On three occasions, namely October 1949, February 1950 and May 1950, the normal sampling units were supplemented by two further sampling units at each position and in each plant type extending from 5 to 10 and 10 to 15 cm. in depth. The results from these samples are presented in Table 4 and Fig. 2. The diagrams appear to show the following points:

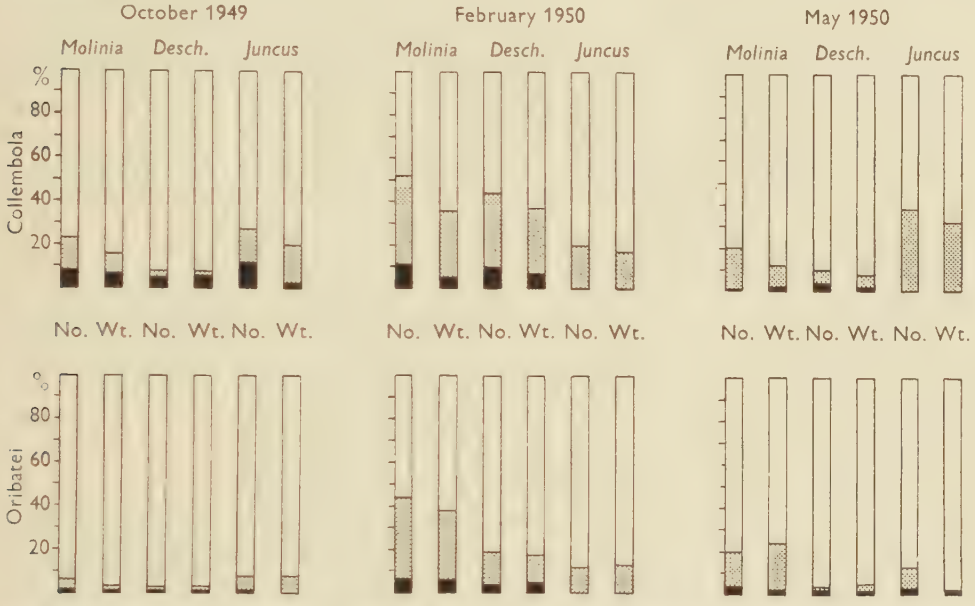

Fig. 2. Numbers and biomass of Collembola and Oribatei on Cothill fen showing depth-distribution on three occasions in three plant types. The upper histograms refer to Collembola, the lower ones to Oribatei. The three groups of six units refer to October, February and May. Within each block of six the first pair are from *Molinia*, the second from *Deschampsia*, the third from *Juncus*. The first member of each pair shows the numbers, the second the biomass. The upper, unshaded portion of each unit shows the proportion of the fauna occurring in the upper 5 cm. of soil, the second (dotted) in the 5–10 cm. layer and the third (black) portion in the 10–15 cm. layer. Each histogram is based on thirty sampling units.

(1) The proportion of the fauna occurring below 5 cm. is usually low, not often above 20% and never above 50% of the total, and decreases further still below 10 cm. This is perhaps a more rapid decrease in the population than is usually found and is presumably associated with the peat subsoil.

(2) There is a considerably higher proportion of animals in the lower layers in February than on the other two occasions. This coincides with the findings of other authors (see p. 104) and is largely the contribution of a limited number of species (See (5) below.)

(3) The proportion of animals in the lower layers is nearly always greater when calculated by numbers than when calculated by biomass; this seems to indicate that the larger species are confined more to the upper layers.

(4) The Oribatei as a whole have a less deep distribution than the Collembola. This also agrees with general opinion, although it may not have been demonstrated before.

(5) From the figures it seems likely that the seasonal fluctuations discussed in the next section would be accentuated rather than reduced if the complete fauna to a depth of 15 cm. were included. Apparently the February figures (the month of highest populations on the fen) should be increased by about 50%, whereas the summer figures should probably have only a few per cent added. This conclusion cannot, of course, be certain since no deep samples were taken in the summer months, but Glasgow's (1939) figures indicate only a single, winter, peak for soil Collembola in the lower layers.

(6) From a faunistic point of view it is clear that, while some species are completely confined to the upper 5 cm. of the soil, others characteristically have a greater range in depth. The following have greater numbers in the 5–10 cm. layer than in the 0–5 cm. layer:

Tullbergia krausbaueri *Isotoma notabilis* *Folsomia listeri*	All three occasions
Nanhermannia elegantula	Nymphs only
Ceratozetes mediocris	February only.

These species alone account for the following proportions of the biomass below 5 cm. in February:

Collembola 5–10 cm. 0·77; 10–15 cm. 0·67.
Oribatei 5–10 cm. 0·79; 10–15 cm. 0·67.

(*d*) *Fluctuations of the fauna in time*

It will be evident from the diagrams and figures already given that there is a marked difference in the size of the fauna as a whole at different times of the year; whether the same precise picture would be repeated every year is open to doubt. However, since the *Molinia* and the *Deschampsia* figures follow the same general trend, the figures for August 1949 are very close to those for August 1950 and, as will be shown later, other authors in Britain have obtained similar results, it appears likely that an August minimum and a maximum early in the year are characteristic of conditions in Britain. A second maximum in May may be more than a chance effect, although in the Collembola it would have been less well marked had the true biomass for each individual been available instead of the mean figure based on an average individual; because, in fact, this sample contained a high proportion of juveniles.

It will be noted that the *Juncus subnodulosus* figures show almost no seasonal trend, and it will be remembered that the *Molinia* and the *Deschampsia* figures are much above those for samples taken at random in the fen; it would therefore be unjustifiable to generalize from these figures and state categorically that a marked seasonal cycle applies to the fen as a whole. Nevertheless, the high proportion of the area covered by the two tussock grasses and the large proportion of the whole fauna which they must contain makes it likely that the mean fauna of the fen, in so far as this abstraction has any meaning, would show similar, if less distinct, periods of high and low numbers.

Comparisons can be made between the histograms for each of the main groups of the fauna and for numbers and biomass. In general, the most conspicuous feature of

the records is the similarity of all the histograms. The scale, however, varies slightly, so that the ratio between August biomass and February biomass is, on the whole, rather greater than between August and February numbers; thus seeming to imply that there is a greater proportion of larger species in the February samples when the population is at its highest. This is shown in Fig. 1 and will be discussed further in § 5. It will be noticed that, both in terms of numbers and of biomass the Collembola are a relatively small constituent of the fauna when compared with the Oribatei; the significance of this will also be considered in § 5 when the results of other studies have been reviewed.

It has already been pointed out that, in so far as the figures for vertical distribution can be relied on, the only occasion when a considerable proportion of the fauna occurs below 5 cm. depth is February. At this time the population is at its highest, so that the ratios indicated by Fig. 1 and Appendix II between the peak figures in February and the minimum figures in August would be considerably greater if the full vertical extent of the fauna were to be included in a future study.

The most surprising feature of the variations in time of the faunistic composition is that almost all species seem to vary in unison; the only definite departures from this generalization would appear to be a few species which seem to have their peak in numbers rather earlier than the rest, including especially *Scheloribates latipes*, whose peak is in December (cf. *Scheloribates laevigatus* whose peak in abundance is at the normal time) and *Oribella paolii* and *Ceratozetes mediocris* which have peaks in November (the latter seems to have a very patchy distribution which may account for apparent peaks in February and June). *Malaconothrus globiger* and *Hypochthoniella pallidula* have ill-defined peaks which are more accurately described as a period of greater abundance throughout the winter and spring. *Nanhermannia elegantula* has a marked additional peak in May and June applying both to the nymphs and the adults. This interesting species has already been noted as having an exceptionally deep vertical range, and no doubt a more detailed study of both vertical and seasonal distribution would be rewarding; it is not at all a widespread species and is only recorded elsewhere in faunistic studies by Van der Drift.

(*e*) *The effect on the fauna of burning the fen*

As explained in the introduction, the investigation was not intended to embrace a study of the effects of burning on the fauna; this was a further factor which was added by outside influences and was mainly regarded as an annoyance in that the already large errors inherent in the material were further increased. On 5 February 1949, one day after the February sampling, the rather dry fen was fired by local people apparently with the intention of driving rabbits from their places of hiding. The fen was not visited for a fortnight after this and it was then noted that while the *Molinia* tussocks and most of the *Molinia* between the tussocks was burned, only the more distal parts of the *Deschampsia* tussocks were burned and the *Juncus subnodulosus* areas did not appear very different from normal apart from the general scattering of ash. By the end of the investigation in the following August little sign of the burning remained. The extent of the burning was mapped and it was found that about one-quarter of the fen remained unburned; this did not appear to differ appreciably from

the remainder before burning but it is the area lying to the south which gradually merges into the *Phragmites communis*-dominated border of one of the streams; it is possible that the water table was slightly higher here and it is certain that *Molinia* tussocks become sparser as the *Phragmites* is approached. At least one of the previous monthly 'positions' must have been situated in this unburned region each month and, as already shown, there was at that time no significant difference in the fauna between 'positions'. For the remaining months of the study the five 'positions' for sampling were divided between the burned and the unburned areas, three and two 'positions' in each area in alternate months. The results given in Table 9 and Fig. 1 are based on the sampling units for the 'burned area' and are to be compared with the Tables 7 and 8, which apply to the 'unburned area' only for March 1950 onwards.

Fig. 1 shows that the immediate effect in March was well marked, in that the *Molinia* tussock fauna was drastically reduced and the *Juncus subnodulosus* fauna considerably increased. The first effect is probably to be expected because the tussocks were severely charred; the second is surprising, indicating, as it does, a rapid migration of animals into the *Juncus subnodulosus* area. Perhaps as surprising is the lack of influence of the burning on the *Deschampsia* tussock fauna and the way in which both *Deschampsia* and *Juncus subnodulosus* faunas are not appreciably different in the burned and unburned areas from April onwards. The recovery of the *Molinia* fauna, too, seems to have been remarkably rapid; in March, April and May the ratios of biomass in the burned as compared with the unburned areas are approximately 28:48:104 for Collembola and 7:59:93 for Oribatei.

From a faunistic point of view, the fauna of the tussocks in March seems to have been fairly normal in composition. The very small *Oppia* species are conspicuous by their absence, and the only species present in considerable numbers are the Collembola (*Isotoma notabilis* being quite exceptionally abundant), and *Notaspis coleoptratus*, *Minuthozetes semirufus*, *Nanhermannia elegantula*, *Oribella paolii*, the Phthiracarids, Parasitids and Eupodids. In the summer months, the fauna in the burned area appears to have remained rather impoverished in the tussocks in June and July; the Collembola perhaps more than the mites. These results, being based on a single incident and very variable material, should not be relied on as typical; should a further study involving the effects of burning, whether by accident or intention, be made, however, it is possible that they will be useful for comparison.

DISCUSSION

The more important results of the present study can be discussed under two headings, faunistic and quantitative. The significance of both is likely to be more easily understood when comparisons are drawn between this fauna and those described by other workers from other habitats. Unfortunately most of the studies which have been made of soil faunas are unsuitable for comparison because the taxonomic separation of the material is very incomplete, because results are not expressed in biomass or respiration rates, or because area is not used as a basis for the expression of the density of the fauna. The studies known to the author in which comparison is possible are those of the following authors: Glasgow (1939), Weis-Fogh (1948), Ford (1935, 1937, 1938), Van Der Drift (1950), Forsslund (1945), Schaller (1950) and Strenzke (1949*a*).

A very brief résumé of the contents of each of these papers from this point of view will be given first and then a comparison of their results will be made under each of the main headings of § 4.

(*a*) *Résumé of authors compared*

Glasgow (1939). This paper is concerned with the Collembola inhabiting the true soil only, and is mainly confined to four species of Onychiuridae. The material was obtained from a meadow. It was found that the abundance of *Onychiurus armatus* was positively correlated with moisture during the wet season; this is not controverted by the inadequate data of the present study.

Ford (1935, 1937, 1938). These papers are based on a water meadow and a meadow containing *Bromus* tussocks. It is probable that Ford's extraction was less efficient than in the present study (Macfadyen, in prep.). The papers are chiefly valuable for the observations on vertical distribution and seasonal variations in the populations of the *Bromus* tussock fauna.

Weis-Fogh (1948) described a very complete investigation of the mites and Collembola in a meadow with a sharp gradient in soil moisture content; he detected a corresponding gradient in a number of animals and showed that the fauna at the two ends was quite different. The area has a deeper soil than Cothill; it was originally a sea beach, and is very sandy. Weis-Fogh distinguished seven distinct floristic types, and there can be no doubt that the area contains a great variety of habitats for the fauna, both for this reason and because there is a wide range in organic matter content, pore space and other factors.

Van Der Drift (1950). This paper is concerned with the fauna of a beech forest and has little in common with the preceding; it is obvious that the fauna is a very poor one both in quantity and in number of species. The study is of interest because biomass figures are calculated and because it shows that there is little seasonal variation in the fauna; a result that will be discussed below.

Schaller (1949) worked on the Collembola only of a renzina soil and of a limestone meadow; his paper includes interesting figures on the depth distribution of the different species.

Forsslund (1945) worked on a considerable variety of soil and vegetation types in forests of Swedish Lapland; the figures are especially interesting in providing comparisons between the soil types but few seasonal comparisons are made and very few samples are taken from each soil type. Forsslund's localities are not easy to compare with those investigated by other workers, and comparison of total faunas is made more difficult because volume and not area is used as a basis of comparison. The separation of the soil layers provides useful information on the preferences of the different species.

Strenzke's (1949*a*) paper is concerned with the Collembola from ten examples of damp soils, mainly lake shores. He investigated the effects of season, soil type and depth on distribution and, owing to his use of the method of sampling already mentioned, was able to estimate density as well as determine the depth range of the different species. An adequate summary of this important paper is not possible here but approximate figures, arrived at by averaging groups of results, are given in the succeeding paragraphs.

Phragmites habitats already mentioned contain fifteen species which include all those common on Cothill in rather similar proportions with the exception of *Onychiurus furcifer*. In fact, Cothill resembles Strenzke's Phragmiteta more closely than any other habitat described in the literature.

Forsslund's figures are based on samples from a wide area; the single *Vaccinium* sampling unit had numbers of species almost equal to those from the whole of the Cothill samples while those from his whole study (in brackets in the Table) are almost twice as high. The most outstanding feature of his figures is the very large count for Trombidiformes (which are not analysed to species). This would appear to be a real difference from all the other studies in the literature, although Forsslund's other samples vary much in this respect. Despite this investigation covering such a wide range of floristic types only ten Oribatei and six Collembola are shared with the Cothill fauna; *Tectocepheus velatus* (only fairly abundant at Cothill) and *Oppia neerlandica* (a rather ubiquitous species) are both common. *Nanhermannia nana* is abundant in deeper layers as is *N. elegantula* at Cothill. *Folsomia quadrioculata* of Cothill appears to be replaced by other members of the genus. It is evident that the Cothill fauna as a whole resembles other areas in the ratio between the number of species in each group except, possibly, in having few Trombidiformes. The detailed species list, however, has little in common with the other areas reviewed and, in fact, the closest resemblance occurs with Van Der Drift's beech forest for Oribatei and Strenzke's Phragmiteta for Collembola.

(*d*) *Distribution in depth*

The Cothill data in this respect are only based on the three sets of sampling units, and it is therefore uncertain whether departures from more detailed studies are fortuitous or a true characteristic of the habitat. On the whole the Collembola agree with other authors' findings and there is little evidence in the literature about the depth distribution of mites. All authors seem to be agreed that the greater part of the fauna is found just at or below the true soil surface in meadow type localities and in the *Fx* layer in raw humus localities such as Van Der Drift's beech forest. Ford, for instance, states that most of the fauna is confined to the upper 1–1½ in. (2·5–3·8 cm.), few animals occur below 4½ in. and none below 8 in.; Acari are normally confined to the upper 1½ in. Glasgow found *Onychiurus ambulans* and *Tullbergia quadrispina* (both absent from Cothill) to be inhabitants of deeper layers and also that *Onychiurus ambulans* has greatest numbers in the deeper layers in February and March (cf. *O. armatus* at Cothill). Ford found the greatest penetration into the soil in February and May. To some extent the Cothill figures agree with these two authors. Forsslund found *Nanhermannia nana* and certain other species which are absent from Cothill to be more abundant in the *H* layer than in the *F* layer. Schaller reports *Tullbergia krausbaueri* to be a deep-living species and this is confirmed by the Cothill records.

Strenzke (1951) states that in north Germany the Oribatids inhabit mainly the surface layers from May to September and move to deeper layers from November to March. He quotes as exceptions two deep-living species which are not found at Cothill. Strenzke (1949*a*) cites *Isotoma* species as being surface-dwelling forms and *Onychiurus armatus* and *Tullbergia krausbaueri* as inhabiting the deeper layers. These

species, with *Folsomia quadrioculata*, are shown to move to deeper layers (below 2·5 cm.) in the winter months, while *Isotoma notabilis* among others does not do this. In this and in finding that in damp conditions the fauna becomes confined to the upper layers he agrees with Agrell (1941).

(*e*) *Variations in time*

The study of time series and the methods for demonstrating recurrent seasonal phenomena belong to a field of statistical science which is not yet satisfactorily explored. By present standards the findings of the paper are quite unable to establish recurrent seasonal cycles if only because they are confined to a single year. However, the coincidence of a number of independent studies by different authors at different times and places would appear to justify some tentative conclusions about this aspect of the results. Glasgow (1939) found peak populations in his Collembola species in February, probably preceded by a maximum in December; Ford (1938) found considerable variation in detail with different species, but concluded that peaks in the same two months separated by lower figures in January are normal for Acari and Collembola; both these authors found an August minimum, and Glasgow also found an April minimum which he correlated with an exceptionally cold period in 1936. The contrast between maximum and minimum is greater in Glasgow's records, being from five to ten times in different species. It is difficult to establish marked seasonal trends in Weis-Fogh's (1948) Danish data owing to rather irregular sampling, but a summer minimum and an autumn maximum are claimed. Weis-Fogh states that the same has also been found by Frenzel (1936) and Baweja (1939); he considers it significant that the autumn maximum should coincide with the period of greatest soil moisture.

Strenzke (1949*a*) found maxima for Collembola tending to be concentrated around July and December but varying in different species; the figures for most species show a maximum between November and February, but *Friesea mirabilis*, *Onychiurus armatus*, *Folsomia quadrioculata* and *Isotoma notabilis* also have July or August maxima. He thus contradicts the results of other continental authors with his July-August maxima as well as with the minima in mid-winter; the summer maxima are also different from the results at Cothill and other British studies. Possibly this is due to the localities being semi-aquatic and probably subject to less extreme climatic conditions. Writing of Oribatei Strenzke (1951) states that August and February minima are usual in north Germany. He also confirms the Cothill results that the faunistic composition varies little through the year. Schaller (1949) found few well-marked seasonal trends and the numbers at the end of his study were on the whole lower than at the beginning a year before; a July and August minimum, and maxima depending on species in October, November and January are indicated by his figures. On the whole, therefore, the present study agrees with all these authors in showing a minimum in August at the end of the summer, and with many of them in finding a maximum in February. The evidence for an earlier maximum in December is limited to a few species, but there is some indication of a later one in May. Van Der Drift (1950) differs from all other authors in finding very little seasonal variation.

It would be premature to make categorical statements about the significance of seasonal fluctuations in the abundance of the soil microfauna, but a few suggestions

seem appropriate here. Most workers seem to assume that climatic factors are mainly responsible, an assumption which is justified by Glasgow's and Ford's and Weis-Fogh's demonstrations of the importance of moisture in particular. The fauna is said to owe its summer minimum to drought and the winter minimum, when it occurs, to cold or to excessive moisture; the autumn maximum or winter maximum are attributed to ideal moisture conditions. The fact that the February maximum seems to be confined to studies in Great Britain, where the winter is very much milder than on the continent of Europe, may indicate that the effect of low temperatures does not operate in the former country. Waksman (1931) and Weis-Fogh (1948) suggest an alternative factor, namely the abundance of food available to the soil organisms. One would expect a rise in the microfauna population at the time when the annual harvest of decaying macroscopic plant matter becomes available to it. Two factors control the time at which this harvest will be reflected in changes in the populations. First, the length of a generation in most Oribatei seems to be of the order of 6 months to a year and in Collembola several months; rapid fluctuations owing to food supply alone are not, therefore, to be expected. Secondly, so far as is known, very few mites and Collembola feed directly on macroscopic plants; the majority appear to eat fungi which attack the decaying plant tissues (Forsslund 1939, 1945; Evans 1951). The fungal attack itself appears to be at least partly dependent on a preliminary mechanical mixing of the plant matter with the soil by earthworms, and possibly woodlice and myriapods. One would therefore expect a considerable delay to occur between the autumn leaf fall and any response by the microfauna population, even if the latter had so evolved that their breeding season allowed a maximum population to coincide with the food maximum. The scarcity of earthworms at Cothill and the resistant nature of the coarse grasses there, which do not appear to become fully incorporated in the soil until late in the spring, might be expected to result in a late peak in the soil population. Whether the peaks in February and May are unique and would not recur in other years or whether they can be explained in such simple terms as food supply and soil moisture it is not at present possible to say; the size of the population will obviously depend on many factors both biotic and physical but it should surely be possible to correlate the very large seasonal variations which seem to be a feature of so many studies, with environmental factors when more and better investigations are available. If the food supply hypothesis is at all tenable, Van Der Drift's finding that beech forest shows little seasonal variation in the size of the microfauna would seem to be explicable on the basis that the litter is constantly present throughout the year but the food supply to the animals is limited by the low rate of bacterial and fungus activity.

It has been noticed that February is the month in which the Cothill samples show the coincidence of three phenomena: (i) a maximum population, (ii) a maximum penetration of the lower layers of the soil, and (iii) a maximum biomass:numbers ratio, implying a higher proportion of larger species. It would therefore appear that in all three respects the habitat is at this time carrying a greater biomass of animals. Whether this coincidence is fortuitous in the third respect can only be seen when other habitats have been investigated; the first two features seem to be well established. If it should prove that this is also a period of abundance of food it would seem to be important that several factors are acting to produce a maximum biomass of animals at

this time. February is also the period of lowest temperatures and therefore, presumably, of low metabolic activity; it is possible therefore that the increase of biomass is a reflexion of greatly reduced intensity of competition for food. Evidently none of these questions can be answered in a satisfactory manner until we have available data from a wide range of habitats, covering as large a proportion of the fauna and flora as possible and combining census figures with those of the metabolic rates of the dominant species in the actual conditions which obtain in nature. When these are available the true contribution of the soil animals to the economy of the dominant vegetation will be apparent, and it will surely be far from insignificant.

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SUMMARY

1. The results of a monthly census of micro-arthropods, repeated for 13 months, in a *Molinia* fen at Cothill, near Oxford, are given.

2. The macroscopic vegetation has a great influence on the density of the fauna, but little effect on its species-composition.

3. The majority of species show no greater variation between adjacent samples than between samples from distant parts of the fen, indicating a very uniform distribution within each plant type.

4. The fauna is largely confined to the upper 5 cm. of the soil, but in winter some species penetrate farther into the soil.

5. Marked but regular seasonal differences in population-size are shown by most species; these involve an August minimum and a February maximum; there are also

lesser maxima for some species in December or May. There is relatively little variation in the species-composition through the year.

6. The effect of an accidental fire on the fen upon the micro-arthropod fauna is described; it was mainly confined to the drier *Molinia* tussocks.

7. Comparison with other published studies on the soil fauna indicates that the fauna at Cothill was unusually rich in individuals. The faunistic composition bears little resemblance to that of other areas studied, but the findings as regards seasonal variation and depth-distribution are similar to those of most other workers. The significance of the seasonal fluctuations is briefly discussed.

8. Throughout the paper biomass figures as well as numbers are given as far as possible; the value of metabolic rate measurements, had they been available, is stressed.

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APPENDIX I. TAXONOMY

A. *Animals determined in detail*

† Species not included in Appendix II and Fig. 1.

ARACHNIDA: ACARINA

ORIBATEI

†*Pelops auritus* C.L.K.
†*Peloptulus phaenotus* (C.L.K.)
Notaspis coleoptratus L.
†*Oribatella berlesi* Mich.
†*Liebstadia similis* (Mich.)
Oribatula tibialis (Nic.)
Scheloribates latipes C.L.K.
S. laevigatus C.L.K.
Minuthozetes semirufus (C.L.K.)
**Ceratozetes mediocris* Berl.
†*C. gracilis* C.L.K.
Euzetes aterrimus C.L.K.
**Humerobates fungorum* L.
Spherozetes orbicularis C.L.K.
Nanhermannia elegantula Berl.
Malaconothrus globiger Träg.
†*Hypocthonius rufulus* C.L.K.
Hypocthoniella pallidula C.L.K.
†*Nothrus palustris* C.L.K.
†*N. bicillatus* C.L.K.
†*Gustavia microcephala* (Nic.)
Cepheus dentatus (Mich.)
Tectocepheus velatus (Mich.)
†**Liacarus coracinus* C.L.K.
†*Belba geniculosa* Oudms.
†*Belba pulverulenta* (C.L.K.)
†*Damaeolus lacinatus* (Berl.)
Oribella paolii Oudms.
†*O. castanea* (Herm.)
Oppia neerlandica Ouds.
O. subpectinata Ouds.
O. bicarinata (Paoli)
†*Ceratoppia bipilis* Herm.
Phthiracarus ligneus Willm.
Hoploderma striculum C.L.K.
†*Suctobelba subtrigona* (Ouds.)

PARASITIFORMES

Geholaspis mandibularis Berl.
Geholaspis sp.
Pergamassus runcatellus Berl.
P. parvulus Berl.
Pachylaelaps lindroffi Sell.
Pachylaelaps sp.
Veigaia nemorensis C.L.K.
Cosmolaelaps vacuus var. *ensiger* Berl.
Cosmolaelaps sp.
Ologamasus pollicipatus var. *appeninorum* Berl.
Dinychus perforatus Kramer (*D. tetraphyllus* Berl.)
Discopoma splendida var.nov.
Discopoma sp.nov.
Urotrachites formicarius Lubb.
Trachytes minima Träg.
Oloviseius minima Kramer
Oloviseius sp.

* See taxonomic notes, p. 111.

APPENDIX II. NUMERICAL DATA

Table 7. *Total numbers of dominant micro-arthropods from the soil of Cothill Fen grouped by months, plant types and species*

(Each figure gives the number per 10 sq.cm. and is the mean of ten observations. *M*, *D* and *J* are the samples from *Molinia*, *Deschampsia* and *Juncus* respectively.)

	August 1949			September 1949			October 1949			November 1949			December 1949			January 1950			February 1950		
	M	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*
Onychiurus armatus } *O. furcifer* }	0·6	0·8	0·3	2·4	0·4	0·2	2·1	1·7	0·6	3·0	1·1	0·6	3·1	1·7	0·8	3·9	2·1	0·9	4·6	4·0	0·2
Tullbergia denisi } *T. krausbaueri* }	0·6	0·1	0·2	4·5	1·4	0·6	4·4	0·4	1·1	7·7	0·3	0·4	2·9	—	3·9	11·1	12·9	2·0	6·0	0·4	1·0
Friesia mirabilis	2·1	1·6	2·0	3·8	2·9	0·4	5·2	3·0	2·6	9·0	3·9	1·6	7·8	5·9	1·9	7·0	13·3	3·3	9·4	4·2	1·2
Folsomia quadrioculata	3·2	3·3	1·4	10·4	3·4	0·7	7·6	9·5	1·9	5·2	4·6	1·5	8·5	8·4	1·2	9·8	10·8	0·7	19·6	18·0	1·4
Isotoma notabilis	1·3	1·1	1·5	0·9	0·7	0·5	1·3	1·4	2·5	1·1	1·2	0·9	0·6	0·2	1·4	1·2	0·8	0·2	1·2	2·6	1·0
Neelus minutus	3·5	0·9	3·9	2·2	1·3	1·5	2·1	0·6	1·5	2·4	—	1·1	2·3	0·2	0·7	1·5	0·1	0·6	1·4	0·6	0·6
Total COLLEMBOLA	11·3	7·8	9·3	24·2	10·1	3·9	22·7	16·6	10·2	28·4	11·1	6·1	25·2	16·4	9·9	34·5	40·0	7·7	42·2	29·8	5·4
Notaspis coleoptratus	1·6	0·9	1·2	0·6	0·2	0·3	1·3	1·0	0·4	1·7	0·4	0·3	2·5	1·9	—	3·6	4·9	1·0	3·8	9·8	0·6
Oribatula tibialis	0·2	0·2	0·1	0·2	0·2	—	2·1	1·2	0·3				2·1	1·9	—	4·7	1·4	—	3·4	2·8	0·6
Scheloribates latipes	1·1	0·5	0·3	0·6	0·2	—	2·4	0·7	0·2	21·6	6·3	2·2	9·6	5·0	0·5	9·1	2·1	0·1	4·0	1·0	—
S. laevigatus	0·4	0·4	0·3	2·0	0·1	0·6	2·1	2·5	1·3				2·7	1·8	0·2	6·6	5·9	1·6	4·6	5·0	0·4
Minuthozetes semirufus	7·3	8·6	1·6	11·4	4·7	0·4	11·2	7·0	1·3	22·1	9·2	3·2	26·1	18·8	—	39·1	15·9	1·3	37·8	21·6	0·6
Ceratozetes mediocris	—	0·1	—	1·9	1·4	—	1·7	4·5	0·4	6·7	12·5	—	0·5	1·0	—	8·3	1·3	—	5·2	7·8	—
Euzetes aterrimus	0·1	0·1	0·2	0·3	—	—	0·9	0·1	0·1	—	—	—	2·4	0·7	0·1	0·3	0·2	0·3	0·8	0·8	—
Sphaerozetes orbicularis	1·0	0·2	0·2	0·5	—	—	3·4	1·7	—	—	—	—	0·9	—	—	0·2	2·3	—	13·4	3·2	1·8
Oribatei nymphs *a*	1·6	1·3	0·8	2·6	1·0	0·3	2·7	2·4	0·4	7·7	4·0	2·0	11·9	4·7	0·5	5·6	5·6	2·3	12·4	10·8	2·2
Oribatei nymphs *b*	5·4	4·1	2·8	6·8	2·8	1·1	6·6	3·6	1·1	—	—	—	4·7	3·2	1·1	5·5	4·4	0·5	25·6	10·2	5·6
Nanhermannia elegantula	0·7	1·0	0·1	6·2	1·2	0·2	4·3	2·0	0·4	4·1	3·8	0·7	9·0	4·7	1·8	6·1	4·0	1·4	17·6	15·2	0·2
Nanhermannia nymphs	2·2	1·2	0·5	19·5	2·2	0·1	6·8	0·1	0·3	13·6	4·3	1·2	18·1	9·7	1·9	10·1	4·7	1·6	8·6	20·0	0·6
Malaconothrus globiger	0·7	0·7	0·1	6·5	0·5	1·2	2·6	—	0·3	5·4	1·3	0·1	0·9	1·2	0·2	3·3	2·1	0·2	7·0	1·6	0·2
Hypocthoniella pallidula	0·5	—	—	3·0	—	—	0·7	—	0·1	8·1	0·4	—	6·5	1·6	—	5·5	2·3	0·1	9·0	1·2	—
Cepheus dentatus	0·1	—	—	—	0·1	—	0·8	0·3	0·5	0·5	—	—	0·5	—	0·3	2·0	—	0·7	—	1·0	—
Tectocepheus velatus	0·1	0·1	0·1	0·1	—	0·1	—	—	0·1	—	—	—	—	—	—	0·6	0·1	—	2·2	0·4	1·0
Oribella paolii	2·6	2·7	0·9	1·3	0·9	0·4	1·0	0·6	1·2	9·9	2·7	0·4	3·0	1·9	1·8	2·2	1·5	1·3	1·4	3·6	0·2
Oppia subpectinata	—	—	—	2·2	0·9	0·1	1·9	0·8	0·5	9·9	4·3	1·0	4·1	1·9	0·1	2·5	1·3	0·2	5·8	3·2	1·2
O. neerlandica	1·9	2·5	0·7	8·2	2·0	0·2	6·6	5·7	0·4	1·9	1·1	0·5	8·4	6·9	0·7	17·7	21·0	1·2	10·6	26·4	—
O. bicarinata	2·0	0·9	0·1	3·9	3·0	0·1	4·9	5·7	0·4	—	—	—	11·1	6·3	0·2	9·7	15·2	1·3	45·8	11·8	1·2
Phthiracacarus ligineus	0·5	0·1	0·5	0·6	0·1	0·2	0·3	0·3	1·4	0·2	0·3	0·3	—	—	0·2	1·4	0·3	0·2	1·4	2·8	0·4
Hoploderma striculum	1·2	0·5	0·9	1·4	0·4	0·9	0·5	0·2	1·3	0·8	0·4	0·4	1·4	0·2	0·2	1·1	0·7	0·2	1·0	2·4	1·0
Total ORIBATEI	31·9	26·6	11·7	80·2	22·0	6·3	65·1	41·5	13·0	115·1	51·3	12·3	127·7	73·8	10·0	147·7	98·4	15·8	223·4	174·4	17·8
Parasitidae, adult	1·5	0·4	0·8	1·6	0·1	0·4	1·1	1·2	0·2	1·3	0·7	0·2	2·0	0·9	0·3	1·9	0·9	0·4	1·2	2·4	—
Parasitidae, nymphs	2·7	1·5	1·8	3·9	1·0	0·2	3·4	4·4	1·0	2·9	1·7	0·1	4·9	1·2	1·2	3·0	1·7	1·4	1·6	3·8	0·2
Discopoma spp.	0·5	—	0·1	0·5	0·1	0·1	0·6	0·4	0·1	0·1	0·1	0·1	0·4	1·0	0·2	0·2	1·5	0·2	1·4	1·1	—
Oloviseius spp.	0·4	0·3	0·4	0·2	0·3	0·1	0·5	0·8	0·1	0·9	0·8	0·3	0·3	0·1	0·1	0·2	0·3	0·2	0·4	1·4	—
Eupodidae	2·6	1·3	1·9	3·0	1·3	0·9	1·8	1·0	1·3	2·9	0·6	0·8	3·6	0·4	0·5	5·8	1·5	1·3	12·6	3·0	0·4
Miscellaneous	4·9	4·3	1·9	7·0	2·8	1·6	5·0	3·3	2·2	8·4	2·1	1·5	3·8	4·4	1·5	2·7	2·7	1·3	12·6	6·4	0·8
Total others	12·6	7·8	6·9	16·2	5·6	3·3	12·4	11·1	4·9	16·5	6·9	3·3	15·0	8·0	3·8	13·8	8·6	4·8	29·8	18·1	1·4
Grand total	55·8	42·2	27·9	120·6	37·7	13·5	100·2	69·2	28·1	160·0	26·4	21·7	167·9	98·2	23·7	196·0	147·0	28·3	295·4	221·4	24·6

Table 7 (*cont.*)

	March 1950			April 1950			May 1950			June 1950			July 1950			August 1950		
	M	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*
Onychiurus armatus	1·8	—	—	0·5	—	—	1·0	0·8	—	—	—	—	—	—	0·2	0·1	0·3	0·4
O. furcifer	3·5	—	0·3	3·0	—	0·3	1·5	1·5	—	0·2	0·2	—	0·8	1·2	0·5	0·3	—	—
Tullbergia denisi	0·5	0·5	—	2·0	0·3	—	0·3	0·5	0·3	4·2	0·2	0·2	1·4	2·4	0·8	0·5	0·8	0·2
T. krausbaueri	0·3	—	0·3	0·5	—	—	—	0·3	3·0	1·6	0·6	0·3	0·6	0·2	0·3	—	0·8	1·0
Friesia mirabilis	2·5	2·0	0·8	6·5	3·3	1·0	3·5	4·3	0·3	3·6	1·4	0·2	2·6	3·6	1·0	0·8	0·3	0·2
Folsomia quadrioculata	7·0	14·3	2·3	16·0	18·5	3·3	13·5	67·5	0·3	11·8	8·6	2·3	5·4	14·6	7·5	5·3	2·0	2·2
Isotoma notabilis	0·8	0·8	—	2·3	0·3	1·5	1·8	5·8	2·0	0·8	0·6	0·5	0·6	0·8	2·0	0·3	0·2	1·8
Neelus minutus	0·8	—	—	0·5	0·5	0·8	0·8	—	0·5	3·0	0·2	0·7	1·0	0·2	1·5	—	0·1	0·2
Total COLLEMBOLA	21·0	20·4	5·0	32·1	22·9	7·2	23·7	81·2	6·4	26·2	12·0	4·2	12·4	23·0	13·8	7·3	4·5	6·0
Notaspis coleoptratus	2·3	3·0	0·3	1·8	0·5	0·8	2·5	2·3	0·5	2·4	1·0	0·8	1·4	1·4	0·2	0·5	1·3	0·2
Oribatula tibialis	0·3	1·3	—	—	—	—	1·5	1·0	1·0	0·2	0·2	—	—	0·6	0·2	0·7	0·3	0·4
Scheloribates latipes	7·5	0·5	—	4·8	—	0·3	2·0	0·3	—	1·2	—	0·2	0·8	0·4	—	1·1	0·5	0·2
S. laevigatus	5·8	7·5	1·0	1·8	3·5	1·5	5·3	0·8	1·3	4·0	2·6	0·3	3·2	4·6	2·2	3·3	1·8	1·2
Minuthozetes semirufus	18·5	33·3	0·8	6·8	1·0	3·3	20·8	1·8	1·5	9·0	2·6	1·7	18·8	8·8	4·3	10·3	2·5	2·2
Ceratozetes mediocris	1·0	—	—	2·5	0·3	0·3	1·8	8·3	—	11·2	4·6	—	—	—	—	—	—	—
Euzetes aterrimus	5·5	—	—	0·3	—	0·5	—	—	0·3	—	—	0·3	—	0·6	0·8	0·3	0·1	0·2
Sphaerozetes orbicularis	8·5	—	—	0·5	0·5	0·5	5·5	0·3	—	1·2	0·4	0·2	1·2	0·4	0·3	—	—	—
Oribatei nymphs *a*	7·5	4·8	—	4·0	5·0	1·3	10·8	1·5	0·3	4·4	2·8	—	13·4	8·0	4·0	4·1	0·7	0·4
Oribatei nymphs *b*	14·5	4·3	2·5	11·5	1·5	5·8	20·3	4·8	1·0	4·4	4·0	0·7	9·2	2·6	2·5	5·7	1·0	1·0
Nanhermannia elegantula	5·0	6·3	0·8	8·5	8·0	1·8	13·3	10·8	1·3	19·4	2·4	0·2	3·8	10·4	0·7	8·0	1·1	2·8
Nanhermannia nymphs	4·5	5·8	1·5	20·3	22·3	3·8	18·3	21·3	0·3	27·2	10·8	0·4	7·6	5·8	4·0	16·1	2·5	1·2
Malaconothrus globiger	6·8	0·3	—	11·3	0·8	—	9·8	2·5	—	9·0	2·2	—	17·6	8·0	1·0	6·6	—	—
Hypocthoniella pallidula	4·3	0·5	—	4·3	2·0	0·3	14·8	0·5	—	15·0	2·2	—	3·6	2·6	—	0·5	0·1	—
Cepheus dentatus	1·0	0·5	—	1·0	—	0·5	0·5	0·3	0·3	0·6	—	0·3	1·2	0·6	0·4	—	—	0·6
Tectocepheus velatus	0·8	0·3	0·5	0·5	—	—	3·3	—	—	0·2	—	0·2	1·2	—	—	—	—	—
Oribella paolii	0·8	1·8	0·5	3·3	1·8	1·0	—	3·0	2·0	0·4	1·2	0·7	1·6	0·8	1·3	0·1	0·1	2·6
Oppia subpectinata	1·5	2·3	0·3	1·0	1·0	—	2·3	0·8	—	—	0·2	—	0·8	0·4	—	0·7	—	—
O. neerlandica	14·8	37·0	1·3	4·3	6·3	0·8	9·5	4·3	0·5	8·2	1·6	—	5·8	5·0	0·5	4·3	5·1	0·3
O. bicarinata	7·3	1·5	—	2·3	2·0	0·5	14·8	8·8	0·8	1·4	0·4	0·2	4·0	3·2	3·3	1·3	6·1	—
Phthiracacarus ligineus	—	0·3	0·5	1·0	—	1·0	0·8	0·3	2·3	1·2	0·4	0·3	0·2	0·4	0·7	0·5	—	—
Hoploderma striculum	2·5	2·0	0·3	1·5	0·3	4·3	2·8	0·3	0·5	1·2	0·4	0·7	0·6	0·6	0·5	—	0·6	—
Total ORIBATEI	129·8	117·3	10·8	95·2	61·1	30·2	168·5	78·4	17·7	127·6	42·6	8·7	102·0	68·6	32·8	66·1	24·5	18·2
Parasitidae, adult	7·0	1·3	0·5	3·5	1·3	2·3	3·3	4·0	1·0	2·2	0·8	0·3	0·6	2·8	1·1	2·3	2·7	1·2
Parasitidae, nymphs	3·0	0·3	1·5	2·8	0·8	0·5	0·8	7·5	0·3	2·0	1·6	0·3	4·4	6·8	3·1	2·0	5·0	1·0
Discopoma spp.	—	3·0	—	0·5	0·8	1·0	2·0	3·0	4·0	0·8	0·2	0·2	0·8	1·6	1·1	0·1	0·1	0·4
Oloviseius spp.	0·8	0·3	—	0·3	—	0·5	0·5	2·3	0·3	0·8	0·2	0·2	1·0	1·4	3·7	0·2	0·5	0·4
Eupodidae	1·3	1·8	0·5	0·5	0·3	1·8	0·3	0·5	0·3	0·8	0·6	1·0	2·0	2·2	2·1	3·0	1·1	2·2
Miscellaneous	1·7	0·5	1·1	0·8	0·9	3·8	2·0	4·3	1·8	3·2	2·2	1·3	1·0	1·2	0·5	2·7	2·7	2·2
Total others	13·8	7·2	3·6	8·4	4·1	9·9	8·9	21·6	7·7	9·8	5·6	3·3	9·8	16·0	11·6	10·3	12·1	7·4
Grand total	164·6	144·9	19·4	135·7	88·1	47·3	201·1	181·2	31·8	163·6	60·2	16·2	124·2	107·6	58·2	83·7	41·1	31·6

APPENDIX II. NUMERICAL DATA

Table 7. *Total numbers of dominant micro-arthropods from the soil of Cothill Fen grouped by months, plant types and species*

(Each figure gives the number per 10 sq.cm. and is the mean of ten observations. *M*, *D* and *J* are the samples from *Molinia*, *Deschampsia* and *Juncus* respectively.)

	August 1949			September 1949			October 1949			November 1949			December 1949			January 1950			February 1950		
	M	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*
Onychiurus armatus } *O. furcifer* }	0·6	0·8	0·3	2·4	0·4	0·2	2·1	1·7	0·6	3·0	1·1	0·6	3·1	1·7	0·8	3·9	2·1	0·9	4·6	4·0	0·2
Tullbergia denisi } *T. krausbaueri* }	0·6	0·1	0·2	4·5	1·4	0·6	4·4	0·4	1·1	7·7	0·3	0·4	2·9	—	3·9	11·1	12·9	2·0	6·0	0·4	1·0
Friesia mirabilis	2·1	1·6	2·0	3·8	2·9	0·4	5·2	3·0	2·6	9·0	3·9	1·6	7·8	5·9	1·9	7·0	13·3	3·3	9·4	4·2	1·2
Folsomia quadrioculata	3·2	3·3	1·4	10·4	3·4	0·7	7·6	9·5	1·9	5·2	4·6	1·5	8·5	8·4	1·2	9·8	10·8	0·7	19·6	18·0	1·4
Isotoma notabilis	1·3	1·1	1·5	0·9	0·7	0·5	1·3	1·4	2·5	1·1	1·2	0·9	0·6	0·2	1·4	1·2	0·8	0·2	1·2	2·6	1·0
Neelus minutus	3·5	0·9	3·9	2·2	1·3	1·5	2·1	0·6	1·5	2·4	—	1·1	2·3	0·2	0·7	1·5	0·1	0·6	1·4	0·6	0·6
Total COLLEMBOLA	11·3	7·8	9·3	24·2	10·1	3·9	22·7	16·6	10·2	28·4	11·1	6·1	25·2	16·4	9·9	34·5	40·0	7·7	42·2	29·8	5·4
Notaspis coleoptratus	1·6	0·9	1·2	0·6	0·2	0·3	1·3	1·0	0·4	1·7	0·4	0·3	2·5	1·9	—	3·6	4·9	1·0	3·8	9·8	0·6
Oribatula tibialis	0·2	0·2	0·1	0·2	0·2	—	2·1	1·2	0·3				2·1	1·9	—	4·7	1·4	—	3·4	2·8	0·6
Scheloribates latipes	1·1	0·5	0·3	0·6	0·2	—	2·4	0·7	0·2	21·6	6·3	2·2	9·6	5·0	0·5	9·1	2·1	0·1	4·0	1·0	—
S. laevigatus	0·4	0·4	0·3	2·0	0·1	0·6	2·1	2·5	1·3				2·7	1·8	0·2	6·6	5·9	1·6	4·6	5·0	0·4
Minuthozetes semirufus	7·3	8·6	1·6	11·4	4·7	0·4	11·2	7·0	1·3	22·1	9·2	3·2	26·1	18·8	—	39·1	15·9	1·3	37·8	21·6	0·6
Ceratozetes mediocris	—	0·1	—	1·9	1·4	—	1·7	4·5	0·4	6·7	12·5	—	0·5	1·0	—	8·3	1·3	—	5·2	7·8	—
Euzetes aterrimus	0·1	0·1	0·2	0·3	—	—	0·9	0·1	0·1	—	—	—	2·4	0·7	0·1	0·3	0·2	0·3	0·8	0·8	—
Sphaerozetes orbicularis	1·0	0·2	0·2	0·5	—	—	3·4	1·7	—	—	—	—	0·9	—	—	0·2	2·3	—	13·4	3·2	1·8
Oribatei nymphs *a*	1·6	1·3	0·8	2·6	1·0	0·3	2·7	2·4	0·4	7·7	4·0	2·0	11·9	4·7	0·5	5·6	5·6	2·3	12·4	10·8	2·2
Oribatei nymphs *b*	5·4	4·1	2·8	6·8	2·8	1·1	6·6	3·6	1·1	—	—	—	4·7	3·2	1·1	5·5	4·4	0·5	25·6	10·2	5·6
Nanhermannia elegantula	0·7	1·0	0·1	6·2	1·2	0·2	4·3	2·0	0·4	4·1	3·8	0·7	9·0	4·7	1·8	6·1	4·0	1·4	17·6	15·2	0·2
Nanhermannia nymphs	2·2	1·2	0·5	19·5	2·2	0·1	6·8	0·1	0·3	13·6	4·3	1·2	18·1	9·7	1·9	10·1	4·7	1·6	8·6	20·0	0·6
Malaconothrus globiger	0·7	0·7	0·1	6·5	0·5	1·2	2·6	—	0·3	5·4	1·3	0·1	0·9	1·2	0·2	3·3	2·1	0·2	7·0	1·6	0·2
Hypocthoniella pallidula	0·5	—	—	3·0	—	—	0·7	—	0·1	8·1	0·4	—	6·5	1·6	—	5·5	2·3	0·1	9·0	1·2	—
Cepheus dentatus	0·1	—	—	—	0·1	—	0·8	0·3	0·5	0·5	—	—	0·5	—	0·3	2·0	—	0·7	—	1·0	—
Tectocepheus velatus	0·1	0·1	0·1	0·1	—	0·1	—	—	0·1	—	—	—	—	—	—	0·6	0·1	—	2·2	0·4	1·0
Oribella paolii	2·6	2·7	0·9	1·3	0·9	0·4	1·0	0·6	1·2	9·9	2·7	0·4	3·0	1·9	1·8	2·2	1·5	1·3	1·4	3·6	0·2
Oppia subpectinata	—	—	—	2·2	0·9	0·1	1·9	0·8	0·5	9·9	4·3	1·0	4·1	1·9	0·1	2·5	1·3	0·2	5·8	3·2	1·2
O. neerlandica	1·9	2·5	0·7	8·2	2·0	0·2	6·6	5·7	0·4	1·9	1·1	0·5	8·4	6·9	0·7	17·7	21·0	1·2	10·6	26·4	—
O. bicarinata	2·0	0·9	0·1	3·9	3·0	0·1	4·9	5·7	0·4	—	—	—	11·1	6·3	0·2	9·7	15·2	1·3	45·8	14·8	1·2
Phthiracacarus ligineus	0·5	0·1	0·5	0·6	0·1	0·2	0·3	0·3	1·4	0·2	0·3	0·3	—	—	0·2	1·4	0·3	0·2	1·4	2·8	0·4
Hoploderma striculum	1·2	0·5	0·9	1·4	0·4	0·9	0·5	0·2	1·3	0·8	0·4	0·4	1·4	0·2	0·2	1·1	0·7	0·2	1·0	2·4	1·0
Total ORIBATEI	31·9	26·6	11·7	80·2	22·0	6·3	65·1	41·5	13·0	115·1	51·3	12·3	127·7	73·8	10·0	147·7	98·4	15·8	223·4	174·4	17·8
Parasitidae, adult	1·5	0·4	0·8	1·6	0·1	0·4	1·1	1·2	0·2	1·3	0·7	0·2	2·0	0·9	0·3	1·9	0·9	0·4	1·2	2·4	—
Parasitidae, nymphs	2·7	1·5	1·8	3·9	1·0	0·2	3·4	4·4	1·0	2·9	1·7	0·4	4·9	1·2	1·2	3·0	1·7	1·4	1·6	3·8	0·2
Discopoma spp.	0·5	—	0·1	0·5	0·1	0·1	0·6	0·4	0·1	0·1	0·1	0·1	0·4	1·0	0·2	0·2	1·5	0·2	1·4	1·1	—
Oloviseius spp.	0·4	0·3	0·4	0·2	0·3	0·1	0·5	0·8	0·1	0·9	0·8	0·3	0·3	0·1	0·1	0·2	0·3	0·2	0·4	1·4	—
Eupodidae	2·6	1·3	1·9	3·0	1·3	0·9	1·8	1·0	1·3	2·9	0·6	0·8	3·6	0·4	0·5	5·8	1·5	1·3	12·6	3·0	0·4
Miscellaneous	4·9	4·3	1·9	7·0	2·8	1·6	5·0	3·3	2·2	8·4	2·1	1·5	3·8	4·4	1·5	2·7	2·7	1·3	12·6	6·4	0·8
Total others	12·6	7·8	6·9	16·2	5·6	3·3	12·4	11·1	4·9	16·5	6·0	3·3	15·0	8·0	3·8	13·8	8·6	4·8	29·8	18·1	1·4
Grand total	55·8	42·2	27·9	120·6	37·7	13·5	100·2	69·2	28·1	160·0	26·4	21·7	167·9	98·2	23·7	196·0	147·0	28·3	295·4	221·4	24·6

Table 7 (*cont.*)

	March 1950			April 1950			May 1950			June 1950			July 1950			August 1950		
	M	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*
Onychiurus armatus	1·8	—	—	0·5	—	—	1·0	0·8	—	—	—	—	—	—	0·2	0·1	0·3	0·4
O. furcifer	3·5	—	0·3	3·0	—	0·3	1·5	1·5	—	0·2	0·2	—	0·8	1·2	0·5	0·3	—	—
Tullbergia denisi	0·5	0·5	—	2·0	0·3	—	0·3	0·5	0·3	4·2	0·2	0·2	1·4	2·1	0·8	0·5	0·8	0·2
T. krausbaueri	0·3	—	0·3	0·5	—	—	—	0·3	3·0	1·6	0·6	0·3	0·6	0·2	0·3	—	0·8	1·0
Friesia mirabilis	2·5	2·0	0·8	6·5	3·3	1·0	3·5	4·3	0·3	3·6	1·4	0·2	2·6	3·6	1·0	0·8	0·3	0·2
Folsomia quadrioculata	7·0	14·3	2·3	16·0	18·5	3·3	13·5	67·5	0·3	11·8	8·6	2·3	5·4	14·6	7·5	5·3	2·0	2·2
Isotoma notabilis	0·8	0·8	—	2·3	0·3	1·5	1·8	5·8	2·0	0·8	0·6	0·5	0·6	0·8	2·0	0·3	0·2	1·8
Neelus minutus	0·8	—	—	0·5	0·5	0·8	0·8	—	0·5	3·0	0·2	0·7	1·0	0·2	1·5	—	0·1	0·2
Total COLLEMBOLA	21·0	20·4	5·0	32·1	22·9	7·2	23·7	81·2	6·4	26·2	12·0	4·2	12·4	23·0	13·8	7·3	4·5	6·0
Notaspis coleoptratus	2·3	3·0	0·3	1·8	0·5	0·8	2·5	2·3	0·5	2·4	1·0	0·8	1·4	1·4	0·2	0·5	1·3	0·2
Oribatula tibialis	0·3	1·3	—	—	—	—	1·5	1·0	1·0	0·2	0·2	—	—	0·6	0·2	0·7	0·3	0·4
Scheloribates latipes	7·5	0·5	—	4·8	—	0·3	2·0	0·3	—	1·2	—	0·2	0·8	0·1	—	1·1	0·5	0·2
S. laevigatus	5·8	7·5	1·0	1·8	3·5	1·5	5·3	0·8	1·3	4·0	2·6	0·3	3·2	4·6	2·2	3·3	1·8	1·2
Minuthozetes semirufus	18·5	33·3	0·8	6·8	1·0	3·3	20·8	1·8	1·5	9·0	2·6	1·7	18·8	8·8	4·3	10·3	2·5	2·2
Ceratozetes mediocris	1·0	—	—	2·5	0·3	0·3	1·8	8·3	—	11·2	4·6	—	—	—	—	—	—	—
Euzetes aterrimus	5·5	—	—	0·3	—	0·5	—	—	0·3	—	—	0·3	—	0·6	0·8	0·3	0·1	0·2
Sphaerozetes orbicularis	8·5	—	—	0·5	0·5	0·5	5·5	0·3	—	1·2	0·4	0·2	1·2	0·4	0·3	—	—	—
Oribatei nymphs *a*	7·5	4·8	—	4·0	5·0	1·3	10·8	1·5	0·3	4·4	2·8	—	13·4	8·0	4·0	4·1	0·7	0·4
Oribatei nymphs *b*	14·5	4·3	2·5	11·5	1·5	5·8	20·3	4·8	1·0	4·4	4·0	0·7	9·2	2·6	2·5	5·7	1·0	1·0
Nanhermannia elegantula	5·0	6·3	0·8	8·5	8·0	1·8	13·3	10·8	1·3	19·4	2·4	0·2	3·8	10·4	0·7	8·0	1·1	2·8
Nanhermannia nymphs	4·5	5·8	1·5	20·3	22·3	3·8	18·3	21·3	0·3	27·2	10·8	0·4	7·6	5·8	4·0	16·1	2·5	1·2
Malaconothrus globiger	6·8	0·3	—	11·3	0·8	—	9·8	2·5	—	9·0	2·2	—	17·6	8·0	1·0	6·6	—	—
Hypocthoniella pallidula	4·3	0·5	—	4·3	2·0	0·3	14·8	0·5	—	15·0	2·2	—	3·6	2·6	—	0·5	0·1	—
Cepheus dentatus	1·0	0·5	—	1·0	—	0·5	0·5	0·3	0·3	0·6	—	0·3	1·2	0·6	0·4	—	—	0·6
Tectocepheus velatus	0·8	0·3	0·5	0·5	—	—	3·3	—	—	0·2	—	0·2	1·2	—	—	—	—	—
Oribella paolii	0·8	1·8	0·5	3·3	1·8	1·0	—	3·0	2·0	0·4	1·2	0·7	1·6	0·8	1·3	0·1	0·1	2·6
Oppia subpectinata	1·5	2·3	0·3	1·0	1·0	—	2·3	0·8	—	—	0·2	—	0·8	0·4	—	0·7	—	—
O. neerlandica	14·8	37·0	1·3	4·3	6·3	0·8	9·5	4·3	0·5	8·2	1·6	—	5·8	5·0	0·5	4·3	5·1	0·3
O. bicarinata	7·3	1·5	—	2·3	2·0	0·5	14·8	8·8	0·8	1·4	0·4	0·2	4·0	3·2	3·3	1·3	6·1	—
Phthiracacarus ligineus	—	0·3	0·5	1·0	—	1·0	0·8	0·3	2·3	1·2	0·4	0·3	0·2	0·4	0·7	0·5	—	—
Hoploderma striculum	2·5	2·0	0·3	1·5	0·3	4·3	2·8	0·3	0·5	1·2	0·4	0·7	0·6	0·6	0·5	—	0·6	—
Total ORIBATEI	129·8	117·3	10·8	95·2	61·1	30·2	168·5	78·4	17·7	127·6	42·6	8·7	102·0	68·6	32·8	66·1	24·5	18·2
Parasitidae, adult	7·0	1·3	0·5	3·5	1·3	2·3	3·3	4·0	1·0	2·2	0·8	0·3	0·6	2·8	1·1	2·3	2·7	1·2
Parasitidae, nymphs	3·0	0·3	1·5	2·8	0·8	0·5	0·8	7·5	0·3	2·0	1·6	0·3	4·4	6·8	3·1	2·0	5·0	1·0
Discopoma spp.	—	3·0	—	0·5	0·8	1·0	2·0	3·0	4·0	0·8	0·2	0·2	0·8	1·6	1·1	0·1	0·1	0·4
Oloviseius spp.	0·8	0·3	—	0·3	—	0·5	0·5	2·3	0·3	0·8	0·2	0·2	1·0	1·4	3·7	0·2	0·5	0·4
Eupodidae	1·3	1·8	0·5	0·5	0·3	1·8	0·3	0·5	0·3	0·8	0·6	1·0	2·0	2·2	2·1	3·0	1·1	2·2
Miscellaneous	1·7	0·5	1·1	0·8	0·9	3·8	2·0	4·3	1·8	3·2	2·2	1·3	1·0	1·2	0·5	2·7	2·7	2·2
Total others	13·8	7·2	3·6	8·4	4·1	9·9	8·9	21·6	7·7	9·8	5·6	3·3	9·8	16·0	11·6	10·3	12·1	7·4
Grand total	164·6	144·9	19·4	135·7	88·1	47·3	201·1	181·2	31·8	163·6	60·2	16·2	124·2	107·6	58·2	83·7	41·1	31·6

Table 8. *Biomass of animals in approximate µg. per* 10 *sq.cm.* (=*mg. per sq.m.*) *of unburned fen*

(Each figure is the mean of ten observations and is calculated from the numbers by means of weighting factors (see text, p. 91). *M*, *D* and *J* are samples from *Molinia*, *Deschampsia* and *Juncus* respectively.)

	August 1949			September 1949			October 1949			November 1949			December 1949			January 1950			February 1950		
	M	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*
Onychiurus armatus } *O. furcifer* }	28·8	38·4	14·4	115·3	19·2	9·6	115·2	81·7	28·8	144·0	53·8	28·8	148·8	81·7	38·4	187·3	100·9	43·2	220·8	192·0	9·6
Tullbergia denisi } *T. krausbaueri* }	0·9	0·2	0·3	6·8	2·1	0·9	6·6	0·6	1·7	11·6	0·5	0·6	4·4	—	5·9	16·7	19·4	3·0	9·0	0·6	1·5
Friesia mirabilis	19·8	15·0	18·8	35·7	27·3	3·7	48·9	28·2	24·4	84·6	36·7	15·0	73·3	55·4	17·9	65·9	125·0	31·0	88·3	39·5	11·3
Folsomia quadrioculata	31·0	32·0	13·6	100·9	33·0	6·8	73·8	92·1	18·4	50·4	44·6	14·6	82·5	81·5	11·7	95·0	104·8	6·8	190·1	174·6	13·6
Isotoma notabilis	7·3	6·2	8·4	5·4	3·9	2·8	7·3	7·8	14·0	6·2	6·7	5·4	3·4	1·1	7·8	6·7	4·5	1·1	6·7	14·6	5·6
Neelus minutus	12·6	3·2	14·1	7·9	4·7	5·4	7·6	2·2	5·4	8·6	—	4·0	8·3	0·7	2·5	5·4	0·4	2·2	5·0	2·2	2·2
Total COLLEMBOLA	100·4	95·0	69·6	272·0	90·2	29·2	259·4	212·6	92·7	305·2	142·3	68·4	320·7	220·4	84·2	377·0	355·0	87·3	519·9	423·5	43·8
Notaspis coleoptratus	39·8	22·4	29·9	14·9	5·0	7·5	32·4	24·9	10·0	42·3	10·0	7·5	62·3	47·3	—	89·6	122·0	24·9	95·6	243·8	14·9
Oribatula tibialis	2·6	2·6	1·3	2·6	2·6	—	27·7	15·8	4·0				27·7	25·0	—	62·0	18·5	—	44·9	37·0	7·9
Scheloribates latipes	16·1	7·3	4·4	18·8	2·9	—	35·0	10·2	2·9	315·5	91·9	32·1	140·2	73·0	7·3	132·8	33·3	1·5	58·4	14·6	—
S. laevigatus	9·3	9·3	7·0	46·6	2·3	14·0	48·9	58·2	30·1				62·9	41·9	4·7	155·0	137·5	37·3	107·2	116·6	9·3
Minuthozetes semirufus	20·4	24·1	4·5	31·9	13·2	1·1	31·4	19·6	3·6	61·8	25·8	9·0	73·2	52·6	—	109·6	44·6	3·6	105·9	60·5	1·7
Ceratozetes mediocris	—	0·5	—	9·1	6·7	—	8·2	21·6	1·9	32·2	60·0	—	2·4	4·8	—	39·8	6·2	—	25·0	37·5	—
Euzetes aterrimus	23·6	23·6	47·2	70·8	—	—	213·0	23·6	23·6	—	—	—	568·0	165·5	23·6	70·8	47·2	70·8	188·2	188·2	—
Sphaerozetes orbicularis	26·5	5·3	5·3	13·3	—	—	90·1	45·0	—	—	—	—	23·9	—	—	5·3	60·9	—	355·0	84·9	47·7
Oribatei nymphs *a*	4·3	3·5	2·2	7·0	2·7	0·8	7·3	6·5	1·1	21·1	10·8	5·4	32·1	12·7	1·4	15·1	15·1	6·2	33·2	29·2	5·9
Oribatei nymphs *b*	12·4	9·4	6·4	15·6	6·4	2·5	15·2	8·3	2·5	—	—	—	10·8	7·4	2·5	12·9	10·1	1·5	60·0	23·4	12·9
Nanhermannia elegantula	6·7	9·5	1·0	58·9	11·4	1·9	40·9	19·0	3·8	38·9	36·1	6·7	85·6	45·7	17·1	57·9	38·0	13·3	167·3	144·4	19·0
Nanhermannia nymphs	11·0	6·0	2·5	97·5	11·0	0·5	34·0	0·5	1·5	68·0	21·5	6·0	91·5	48·5	9·5	50·5	23·5	8·0	43·0	100·0	3·0
Malaconothrus globiger	2·8	2·8	0·4	26·0	2·0	4·8	10·4	—	1·2	21·6	5·2	0·4	3·6	4·8	0·8	13·2	8·4	0·8	28·0	6·4	0·8
Hypocthoniella pallidula	1·7	—	—	10·2	—	—	2·4	—	0·3	27·6	13·6	—	22·1	5·4	—	18·7	7·8	0·3	30·6	3·8	—
Cepheus dentatus	7·5	—	—	—	7·5	—	60·0	22·5	37·5	37·5	—	—	37·5	—	22·5	150·0	—	52·5	—	75·0	—
Tectocepheus velatus	0·3	0·3	0·3	0·3	—	0·3	—	—	0·3	—	—	—	—	—	—	1·6	0·3	—	5·7	1·0	2·6
Oribella paolii	12·0	12·4	4·1	6·0	4·1	1·8	4·6	2·8	5·5	45·6	12·4	1·8	13·8	8·7	8·3	10·1	6·9	6·0	6·4	16·6	0·9
Oppia subpectinata	—	—	—	5·9	2·4	0·3	5·1	2·2	1·4	26·9	11·6	2·7	11·1	5·1	0·3	6·8	3·5	0·5	15·7	8·7	3·2
O. neerlandica	2·9	3·8	1·1	12·3	3·0	0·3	9·9	8·6	0·6	2·9	1·7	0·8	12·6	10·4	1·1	26·8	31·5	1·8	15·9	39·6	—
O. bicarinata	1·0	0·5	0·1	2·0	1·5	0·5	2·5	2·9	0·2	—	—	—	5·6	3·2	0·1	4·9	7·6	0·7	22·9	7·4	0·6
Phthiracacarus ligineus	3·0	0·6	3·0	3·5	0·6	1·2	1·8	1·8	8·3	1·2	1·8	1·8	—	—	1·2	8·3	1·8	1·2	8·3	16·5	2·4
Hoploderma striculum	16·9	6·5	11·7	18·3	5·2	11·7	6·5	2·6	17·0	10·4	5·2	5·2	18·2	2·6	2·6	14·3	9·1	2·6	13·0	31·2	13·0
Total ORIBATEI	220·8	150·4	132·4	461·4	90·5	49·2	687·3	296·6	157·3	753·5	307·6	79·4	1305·1	564·6	103·0	1056·0	633·8	233·5	1430·2	1286·3	145·8
Parasitidae, adult	75·0	20·0	40·0	80·0	5·0	20·0	55·0	60·0	10·0	65·0	35·0	10·0	100·0	45·0	15·0	95·0	45·0	20·0	60·0	120·0	—
Parasitidae, nymphs	90·0	50·0	60·0	130·0	33·3	7·3	113·3	146·7	33·3	96·7	56·7	13·3	163·3	40·0	40·0	100·0	56·7	46·7	53·3	126·7	6·7
Discopoma spp.	12·2	—	2·4	11·2	2·4	2·4	14·6	9·7	2·4	2·4	2·4	2·4	9·7	24·3	4·9	4·9	36·5	4·9	34·0	26·7	—
Oloviseius spp.	13·3	10·0	13·3	6·7	10·0	3·3	16·7	26·7	3·3	30·0	26·7	10·0	10·0	3·3	3·3	6·7	10·0	6·7	13·3	46·7	—
Eupodidae	6·0	3·0	4·4	6·9	3·0	2·1	4·1	2·3	3·0	6·7	1·4	1·8	8·3	9·2	1·2	13·3	3·5	3·0	29·0	6·9	0·9
Total others	196·5	83·0	120·1	235·8	53·7	35·1	203·7	245·4	52·0	200·8	122·2	37·5	201·3	121·8	64·4	219·9	151·7	81·3	189·6	327·0	7·6
Grand total	517·7	328·4	322·1	945·8	244·4	113·5	1150·4	754·6	302·0	1259·5	572·1	185·3	1917·1	906·8	251·6	1597·1	1140·5	402·1	2139·7	2036·8	197·2

Table 8 (*cont.*)

	March 1950			April 1950			May 1950			June 1950			July 1950			August 1950		
	M	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*	*M*	*D*	*J*
Onychiurus armatus	86·4	—	—	24·0	—	—	48·0	38·4	—	—	—	—	—	—	9·6	4·8	14·4	19·2
O. furcifer	168·1	—	14·4	144·0	—	14·4	72·0	72·0	—	9·6	9·6	—	38·4	57·6	24·0	14·4	—	—
Tullbergia denisi	0·8	0·8	—	3·0	0·5	—	0·5	0·8	0·5	6·3	0·3	0·3	2·1	3·6	1·2	0·8	1·2	0·3
T. krausbaueri	4·1	—	4·1	6·9	—	—	—	4·1	41·4	22·1	8·3	4·1	8·3	2·8	4·1	—	11·0	13·8
Friesia mirabilis	23·5	18·8	7·5	61·1	31·3	9·4	32·9	40·4	2·8	33·8	13·2	1·9	24·4	33·8	9·4	7·5	2·8	1·9
Folsomia quadrioculata	67·8	138·8	22·3	155·2	179·5	32·0	131·0	654·5	2·9	111·4	83·4	22·3	52·4	141·7	72·8	51·4	19·4	21·4
Isotoma notabilis	4·5	4·5	—	12·9	1·7	8·4	10·1	32·5	11·2	4·5	3·4	2·8	3·4	4·5	11·2	1·7	1·1	10·1
Neelus minutus	2·9	—	—	1·8	1·8	2·9	2·9	—	1·8	10·8	0·7	2·5	3·6	0·7	5·4	-	0·4	0·7
Total COLLEMBOLA	358·1	162·9	48·3	408·9	214·8	67·1	297·4	842·7	60·6	201·5	118·9	33·9	132·6	244·7	137·7	80·6	50·3	67·4
Notaspis coleoptratus	57·3	74·7	7·5	44·8	12·5	19·9	62·3	57·3	12·5	59·9	24·9	19·9	34·9	34·9	5·0	12·5	32·4	5·0
Oribatula tibialis	4·0	17·2	—	—	—	—	19·8	13·2	13·2	2·6	2·6	—	—	7·9	2·6	9·2	4·0	5·3
Scheloribates latipes	109·6	7·3	—	70·1	—	4·4	29·2	4·4	—	17·5	—	2·9	11·7	5·8	—	16·1	7·3	2·9
S. laevigatus	135·1	174·8	23·3	41·9	81·5	34·9	123·5	18·6	30·3	93·2	60·6	7·0	74·6	107·2	51·2	76·8	41·9	27·9
Minuthozetes semirufus	51·7	93·2	2·2	19·0	2·8	9·2	58·3	5·0	4·2	25·2	7·3	4·8	52·7	24·6	12·0	28·8	7·0	6·2
Ceratozetes mediocris	4·8	—	—	12·0	1·4	1·4	8·6	39·9	—	53·8	22·1	—	—	—	—	—	—	—
Euzetes aterrimus	130·0	—	—	70·8	—	118·2	—	—	70·8	—	—	70·8	—	141·8	188·2	70·8	23·6	47·2
Sphaerozetes orbicularis	225·2	—	—	13·3	13·3	13·3	145·8	8·0	—	31·8	10·6	5·3	31·8	10·6	8·0	—	—	—
Oribatei nymphs *a*	20·3	13·0	—	10·8	13·5	3·5	29·2	4·1	0·8	11·9	7·6	—	35·6	21·6	10·8	11·1	1·9	1·1
Oribatei nymphs *b*	33·4	9·9	5·8	76·4	3·5	13·3	47·2	11·0	2·3	10·1	9·2	1·6	21·1	6·0	5·8	13·1	2·3	2·3
Nanhermannia elegantula	47·5	59·9	7·6	80·8	76·0	17·1	126·4	102·7	12·4	189·3	22·8	1·9	36·1	98·8	6·7	76·0	10·5	26·6
Nanhermannia nymphs	22·5	29·0	7·5	101·5	111·5	19·0	91·5	106·5	1·5	136·0	54·0	2·0	38·0	29·0	20·0	80·5	12·5	6·0
Malaconothrus globiger	27·2	1·2	—	38·2	3·2	—	39·2	10·0	—	26·8	8·8	—	72·0	29·2	4·0	23·8	—	—
Hypocthoniella pallidula	14·6	1·7	—	14·8	6·8	1·1	50·3	1·7	—	47·4	7·5	—	12·2	8·9	—	1·7	0·3	—
Cepheus dentatus	75·0	37·5	—	75·0	—	37·5	37·5	22·5	22·5	45·0	—	22·5	90·0	45·0	30·0	—	—	45·0
Tectocepheus velatus	2·1	7·8	1·3	1·3	—	—	8·6	—	—	0·5	—	0·5	3·1	—	—	—	—	—
Oribella paolii	3·7	8·3	2·3	15·2	8·3	4·6	—	13·8	9·2	1·8	5·5	3·2	7·4	3·7	6·0	0·5	0·5	12·0
Oppia subpectinata	4·1	6·2	0·8	2·7	2·7	—	6·2	2·2	—	—	0·5	—	2·2	1·1	—	1·9	—	—
O. neerlandica	22·2	55·5	2·0	6·5	9·5	1·2	14·3	6·5	0·8	12·3	2·4	—	8·7	7·5	0·8	6·5	7·7	0·5
O. bicarinata	3·7	0·8	—	1·2	1·0	0·3	7·4	4·4	0·4	0·7	0·2	0·1	2·0	1·6	1·7	0·7	3·1	—
Phthiracacarus ligineus	—	1·8	3·0	5·9	—	5·9	4·7	1·8	13·6	7·1	2·3	1·8	1·2	2·4	4·1	3·0	—	—
Hoploderma striculum	32·5	26·0	3·9	19·5	3·9	55·9	36·4	3·9	6·5	15·6	5·2	9·1	7·8	7·8	6·5	--	—	7·8
Total ORIBATEI	1026·5	625·8	67·2	721·5	351·4	360·7	946·4	437·5	201·0	788·5	254·1	153·4	543·1	595·4	363·4	433·0	155·0	195·8
Parasitidae, adult	35·0	65·0	25·0	175·0	65·0	115·0	165·0	200·0	50·0	110·0	40·0	15·0	30·0	140·0	55·0	115·0	135·0	60·0
Parasitidae, nymphs	100·0	10·0	50·0	93·3	26·7	16·7	26·7	250·0	10·0	66·7	53·3	10·0	146·7	226·7	103·3	66·7	166·7	33·3
Discopoma spp.	—	29·2	—	12·2	19·4	24·3	48·6	72·9	97·3	19·4	4·9	4·9	19·4	38·9	26·8	2·4	2·4	9·7
Oloviseius spp.	26·7	10·0	—	10·0	—	16·7	16·7	16·7	10·0	26·7	6·7	6·7	33·3	46·7	123·3	6·7	16·7	13·3
Eupodidae	3·0	4·1	1·2	1·2	0·7	4·1	0·7	1·2	0·7	1·8	1·4	2·3	4·6	5·1	4·8	6·9	2·5	5·1
Total others	164·7	118·3	76·2	291·7	111·8	176·8	257·7	540·8	168·0	224·6	106·3	38·9	234·0	457·4	313·2	197·7	323·3	121·4
Grand total	1549·3	907·0	191·7	1361·3	678·0	604·6	1501·5	1881·0	429·6	1194·6	479·3	226·2	909·7	1297·5	814·3	711·3	528·6	344·1

Table 9. *Summary of numbers and weights of mites and Collembola from burned area only*

(Numbers and weights (μg.) are per 10 sq.cm. *M*, *D* and *J* refer to the three plant types, *Molinia*, *Deschampsia* and *Juncus* respectively.)

	March 1950						April 1950						May 1950					
	M		*D*		*J*		*M*		*D*		*J*		*M*		*D*		*J*	
	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Onychiurus armatus	—	—	0·4	19·2	0·2	9·6	1·0	48·0	1·2	57·6	0·3	14·4	1·0	48·0	—	—	0·5	24·0
O. furcifer	0·6	28·8	1·2	57·5	1·5	72·0	0·3	14·4	0·2	9·6	—	—	1·5	72·0	2·0	96·0	—	—
Tullbergia denisi	0·2	0·3	0·4	0·6	1·3	2·0	1·3	2·0	0·3	0·5	0·3	0·5	6·0	9·0	0·5	0·8	0·3	0·4
T. krausbaueri	0·6	8·3	1·2	16·6	0·3	4·1	—	—	—	—	0·2	2·8	1·8	24·2	—	—	—	—
Friesia mirabilis	1·6	15·0	5·8	54·5	6·3	59·2	3·5	33·0	3·5	33·0	1·7	16·0	2·8	25·8	1·8	16·5	0·5	4·7
Folsomia quadrioculata	2·8	27·2	7·2	69·8	10·8	104·8	8·5	82·5	27·3	265·0	2·0	19·4	11·8	114·0	15·0	145·7	1·3	12·3
Isotoma notabilis	3·6	20·1	0·4	2·2	1·0	5·6	2·8	15·7	0·2	1·1	1·0	5·6	1·8	9·8	2·0	11·2	—	—
Neelus minutus	0·4	1·4	0·2	0·7	1·0	3·6	0·2	0·7	—	—	1·3	4·7	1·5	5·4	0·5	1·8	—	—
Total COLLEMBOLA	9·8	101·1	16·8	221·1	22·4	260·9	17·6	196·3	32·7	366·8	6·8	63·4	28·2	308·2	21·8	272·0	2·6	41·4
Notaspis coleoptratus	1·2	29·8	2·8	69·7	1·3	31·4	2·7	67·3	3·0	74·8	0·3	7·5	3·3	80·9	1·3	31·1	0·3	6·2
Oribatula tibialis	—	—	0·8	10·6	1·3	17·2	—	—	0·2	2·6	—	—	0·3	3·3	0·5	6·6	—	—
Scheloribates latipes	—	—	1·0	14·6	1·2	17·5	0·5	7·3	—	—	—	—	0·3	3·7	1·0	14·6	—	—
S. laevigatus	0·8	18·6	5·2	118·8	3·8	88·6	2·0	46·6	1·2	28·0	0·2	4·7	2·5	58·3	0·3	5·8	—	—
Minuthozetes semirufus	1·4	3·9	20·2	56·6	20·2	56·6	4·3	12·0	2·7	7·6	2·2	6·2	19·0	53·2	2·5	7·0	—	—
Ceratozetes mediocris	—	—	0·2	1·0	2·0	9·6	2·7	13·0	0·2	1·0	6·2	29·8	6·3	30·0	—	—	—	—
Euzetes aterrimus	—	—	—	—	0·3	70·9	—	—	0·2	47·3	—	—	0·8	177·3	0·3	59·2	—	—
Sphaerozetes orbicularis	—	—	—	—	7·0	185·5	1·5	39·8	—	—	—	—	4·3	112·7	—	—	—	—
Oribatei nymphs *a*	2·4	6·5	7·2	19·4	10·0	27·0	8·7	23·5	1·2	3·2	0·7	1·9	4·5	12·2	1·3	3·4	—	—
Oribatei nymphs *b*	0·8	1·8	3·0	6·9	41·0	94·3	7·5	17·3	1·5	3·5	0·7	1·6	14·5	33·3	1·8	4·0	—	—
Nanhermannia elegantula	0·4	3·8	5·6	53·3	12·5	118·8	2·3	21·8	5·2	49·4	0·5	4·8	5·0	47·5	9·5	90·2	0·5	4·8
Nanhermannia nymphs	0·6	3·0	10·6	53·0	18·2	91·0	10·0	51·0	13·2	67·3	1·2	6·1	10·8	54·8	8·3	42·1	0·3	1·3
Malaconothrus globiger	—	—	0·6	2·4	10·2	40·8	3·5	14·0	0·2	0·8	0·2	0·8	10·8	43·0	0·5	2·0	—	—
Hypocthoniella pallidula	—	—	0·4	1·4	18·0	61·2	2·2	7·5	0·3	1·0	—	—	7·8	26·4	1·5	5·1	—	—
Cepheus dentatus	—	—	—	—	1·0	75·0	0·3	22·5	—	—	—	—	1·0	75·0	0·3	18·8	—	—
Tectocepheus velatus	—	—	0·4	1·0	5·0	13·0	0·2	0·5	—	—	—	—	—	—	—	—	—	—
Oribilla paolii	1·2	5·5	6·8	31·3	3·0	13·8	2·2	10·1	3·7	17·0	1·2	5·5	2·8	12·7	1·3	5·8	0·3	1·2
Oppia subpectinata	—	—	0·6	1·6	2·3	6·2	1·8	4·9	0·5	1·4	0·2	0·5	1·0	2·7	1·0	2·7	—	—
O. neerlandica	—	—	8·6	12·9	9·7	14·6	10·8	16·2	7·8	11·7	0·2	0·3	11·3	16·9	9·3	13·9	—	—
O. bicarinata	—	—	3·8	1·9	15·3	7·7	13·7	6·9	4·8	2·4	0·2	0·1	14·5	7·3	5·3	2·7	0·3	0·1
Phthiracacarus ligineus	0·2	1·2	0·8	4·7	2·3	13·6	—	—	—	—	0·2	1·2	—	—	—	—	—	—
Hoploderma striculum	0·2	2·6	0·6	7·8	1·8	23·4	3·3	42·9	0·2	2·6	0·2	2·6	2·3	29·3	0·5	6·5	0·8	9·8
Total ORIBATEI	9·2	76·7	78·2	468·9	187·4	1077·7	81·2	425·1	48·1	321·6	14·4	73·6	123·1	880·5	46·5	321·5	2·5	23·4
Parasitidae, adult	3·4	170·0	2·6	130·0	3·2	160·0	5·2	260·0	1·0	50·0	1·5	75·0	3·8	187·5	4·5	225·0	1·0	50·0
Parasitidae, nymphs	1·0	33·3	1·8	60·0	2·8	93·3	2·3	76·7	4·8	160·0	1·0	33·3	—	—	—	—	—	—
Discopoma spp.	0·4	9·7	0·4	9·7	4·7	114·2	0·3	7·3	0·5	12·2	0·2	4·9	3·5	85·0	1·3	30·8	—	—
Oloviseius spp.	0·8	26·7	0·8	26·7	1·5	50·0	0·5	16·7	0·7	23·3	0·5	16·7	3·3	108·7	1·5	50·0	0·3	8·3
Eupodidae	1·2	2·8	0·4	0·9	2·2	5·1	3·0	6·9	0·2	0·5	1·2	2·8	2·3	5·2	1·0	2·3	0·5	1·2
Total others	6·8	242·5	6·0	227·3	14·4	422·6	11·3	367·6	7·2	246·0	4·4	132·7	12·9	386·4	8·3	308·1	1·8	59·5
Grand total	25·8	420·3	101·0	917·3	224·2	1761·2	110·1	989·0	88·0	934·4	25·6	269·7	164·2	1575·1	76·6	901·6	6·9	124·3

Table 9 (*cont.*)

	June 1950						July 1950						August 1950					
	M		*D*		*J*		*M*		*D*		*J*		*M*		*D*		*J*	
	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Onychiurus armatus	—	—	—	—	0·5	24·0	0·5	24·0	—	—	—	—	—	—	0·7	32·2	—	—
O. furcifer	—	—	—	—	0·3	12·0	—	—	0·3	12·0	0·5	24·0	0·3	14·4	0·3	14·4	—	—
Tullbergia denisi	1·0	1·5	0·5	0·8	—	—	0·3	0·4	0·5	0·8	0·3	0·4	2·3	3·5	0·7	1·0	0·8	1·1
T. krausbaueri	—	—	—	—	0·5	6·9	—	—	0·3	3·5	0·3	3·5	—	—	0·3	4·1	0·5	6·9
Friesia mirabilis	1·5	14·1	1·8	16·5	1·8	16·5	1·3	11·8	2·5	23·5	1·3	11·8	3·0	28·2	4·7	45·0	0·3	2·8
Folsomia quadrioculata	5·0	48·5	12·0	116·3	2·0	19·4	2·3	21·8	25·0	242·5	1·8	17·0	1·7	16·2	12·0	116·3	0·5	4·9
Isotoma notabilis	—	—	0·8	4·2	1·0	5·6	0·3	1·4	2·3	12·6	0·3	1·4	0·3	1·7	3·0	16·8	0·8	4·2
Neelus minutus	0·8	2·7	—	—	1·3	4·5	0·3	0·9	0·3	0·9	0·8	2·7	0·3	1·1	—	—	1·3	4·5
Total COLLEMBOLA	8·3	66·8	14·1	137·8	7·4	88·9	5·0	60·3	31·2	295·8	5·2	60·8	7·9	65·1	21·7	229·8	4·2	24·4
Notaspis coleoptratus	1·3	31·1	1·3	31·1	—	—	2·0	49·8	2·3	56·0	0·8	17·4	2·3	57·3	4·3	107·2	1·3	31·1
Oribatula tibialis	0·3	3·3	0·5	6·6	1·3	17·5	—	—	0·3	3·3	0·3	3·3	—	—	0·7	8·8	—	—
Scheloribates latipes	0·3	3·7	0·3	3·7	0·3	3·7	0·3	3·7	—	—	0·3	3·7	—	—	—	—	0·3	3·7
S. laevigatus	1·0	23·3	2·3	52·4	—	—	4·0	93·2	2·5	58·3	0·5	11·7	3·3	77·5	2·3	53·6	1·3	29·1
Minuthozetes semirufus	4·5	12·6	2·8	7·7	1·5	4·2	7·0	19·6	10·3	28·7	0·8	2·1	4·0	11·2	8·7	24·3	3·5	9·8
Ceratozetes mediocris	0·3	1·2	0·3	1·2	—	—	0·3	1·2	—	—	0·3	1·2	—	—	—	—	—	—
Euzetes aterrimus	—	—	0·3	59·2	0·3	59·2	0·5	118·2	—	—	0·3	59·2	0·3	70·9	—	—	0·3	59·2
Sphaerozetes orbicularis	0·8	19·9	—	—	0·3	6·6	—	—	—	—	—	—	—	—	2·7	70·8	—	—
Oribatei nymphs *a*	4·5	12·2	5·0	13·5	0·8	2·0	13·5	36·5	9·0	24·3	1·8	4·7	5·3	14·3	10·3	27·8	1·8	4·7
Oribatei nymphs *b*	10·5	24·2	4·5	10·3	3·0	6·9	8·0	18·4	3·8	8·6	1·8	4·0	2·0	4·6	8·0	18·4	1·0	2·3
Nanhermannia elegantula	1·3	11·9	4·0	38·0	0·3	2·4	1·3	11·9	1·0	9·5	0·3	2·4	4·0	38·0	16·7	158·3	2·5	23·8
Nanhermannia nymphs	6·3	31·9	7·0	35·7	1·5	7·7	6·5	33·2	6·3	31·9	1·8	8·9	10·3	52·5	25·7	131·3	2·3	14·0
Malaconothrus globiger	1·5	6·0	0·3	1·0	0·3	1·0	6·5	26·0	6·0	24·0	4·0	16·0	4·3	17·2	17·0	68·0	1·0	4·0
Hypocthoniella pallidula	0·3	0·9	—	—	—	—	0·8	2·6	0·8	2·6	—	—	1·3	4·4	0·3	1·0	—	—
Cepheus dentatus	1·3	93·8	0·3	18·8	0·5	37·5	0·3	18·8	1·0	75·0	—	—	—	—	0·7	50·0	—	—
Tectocepheus velatus	—	—	—	—	0·3	0·7	0·3	0·7	—	—	—	—	—	—	—	—	0·3	0·7
Oribilla paolii	1·0	4·6	0·5	2·3	1·0	4·6	0·3	1·2	1·0	4·6	1·5	6·9	—	—	1·0	4·6	1·8	8·0
Oppia subpectinata	—	—	—	—	—	—	—	—	0·3	0·7	—	—	2·0	5·4	—	—	—	—
O. neerlandica	2·5	3·8	2·5	3·8	1·0	1·5	5·3	7·9	5·8	8·6	0·5	0·8	8·0	12·0	33·0	50·0	0·5	0·8
O. bicarinata	—	—	5·5	2·8	—	—	1·3	0·6	4·3	2·1	0·3	0·1	1·7	0·8	12·7	6·3	0·5	0·3
Phthiracacarus ligineus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hoploderma striculum	2·0	26·0	0·5	6·5	1·5	19·5	1·3	16·3	0·8	9·8	1·3	16·3	0·3	3·9	2·3	30·0	—	—
Total ORIBATEI	39·8	310·4	37·9	294·6	13·9	175·0	59·5	459·8	55·5	348·0	16·6	158·7	49·3	370·0	146·4	810·4	17·9	191·5
Parasitidae, adult	0·3	12·5	0·5	25·0	1·3	62·5	1·5	75·0	1·8	87·5	0·5	25·0	1·3	65·0	1·7	83·5	1·3	62·5
Parasitidae, nymphs	0·5	16·7	4·3	141·7	0·5	16·7	6·0	200·0	2·5	83·3	1·5	50·0	3·7	122·3	18·7	622·3	0·5	16·7
Discopoma spp.	0·5	12·2	—	—	0·8	18·2	—	—	—	—	—	—	0·3	7·3	1·0	24·3	—	—
Oloviseius spp.	—	—	—	—	0·3	8·3	0·5	16·7	1·0	33·3	1·8	58·3	—	—	2·7	89·0	1·0	33·3
Eupodidae	1·5	3·5	0·3	0·6	1·3	2·9	3·5	8·1	2·0	4·6	1·5	3·0	5·3	12·2	6·0	13·8	5·0	11·5
Total others	2·8	44·9	5·1	167·3	4·2	108·6	11·5	299·8	7·3	208·7	5·3	136·3	10·6	206·8	30·1	832·9	7·8	124·0
Grand total	50·9	422·1	57·1	599·7	25·5	372·5	76·0	819·9	94·0	852·5	27·1	355·8	67·8	641·9	198·2	1873·1	29·9	339·9

A THERMAL RACE OF *DAPHNIA ATKINSONI* BAIRD, AND ITS DISTRIBUTIONAL SIGNIFICANCE

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Races of Cladocera showing unusual sensitivity or resistance to high temperatures have been reported on a number of occasions (Brown 1929; Banta & Wood 1928; Banta 1939; Wood & Banta 1929). Huxley (1942, pp. 52, 60) has commented on the potential evolutionary significance of one of these thermal races, but the actual reports refer mainly to laboratory strains, and have no distributional significance beyond indicating the habitat potentialities of the species.

In the course of work on the thermal resistance of Cladocera, using animals collected in the field, I have discovered a thermal race of *Daphnia atkinsoni* Baird, which is of considerable interest because of its bearing on distributional problems. The experiments were conducted to determine the temperature at which 50% mortality occurred on 24 hr. exposure (details of the method are contained in a paper in the press). For specimens of the low-temperature race obtained from Berrylands, Surrey, this lethal point was about 26·8° C.† In all other races of species of *Daphnia* which I have investigated the lethal point was over 30° C., and for a 'normal' race of *D. atkinsoni* occurring at Godshill, Hampshire, it was $32{\cdot}9 \pm 0{\cdot}2$° C.

It is noteworthy that the low-temperature race showed a reproductive behaviour almost identical with that reported by Banta (1939) for his low-temperature race of *Daphnia pulex* (De Geer) which forms ephippia and reproduces sexually with such great readiness at 20° C., even in the presence of an adequate food supply, that it is impossible to maintain parthenogenetic clones at such a high temperature, though they can be maintained at lower temperatures. The 'normal' race from Hampshire, on the other hand, shows no reproductive peculiarities. The Berrylands race inhabits a temporary pool which dries up in early summer. It is present in this pool throughout the winter, producing young in all months, but the population dies out in early summer. The reproductive behaviour is thus well adapted to the nature of the habitat.

This race is of special interest since *D. atkinsoni* is one of a small group of entomostracans which are generally considered to be southern, warm-water species, and which are only reported sporadically and somewhat infrequently from north and west Europe. It has been suggested that the distribution of these species is controlled by temperature, and that they only occur accidentally in northern countries (Mathias 1937). Fox (1949) has brought forward evidence that one of these, *Triops cancriformis* (Bosc), is really permanently established in England, and the same is probably true of *Chirocephalus diaphanus* (Prévost), and the species of *Moina* (general records). Berg (1931) considered that *Daphnia atkinsoni* was a normal element of the Danish

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† Owing to the fact that the temperature-mortality curve is not of the normal shape, no standard error can be given.

fauna, but thought that it required high temperatures. The low-temperature race appears to be the commonest form in western Europe. Prof. Berg has informed me that, with a single exception, all the populations of this species which he has investigated die down in summer. Similarly, Dr A. Pacaud (in litt.) has never found this species living at high temperatures. It is not possible to suggest an alternative explanation for the rarity of this species in north-west Europe, or for its restriction to those ponds which reach the highest temperatures in summer; but the temperature explanation is certainly not true. On the other hand, temperature may be the limiting factor for such species as *Moina macrocopa* (Straus) which are very susceptible to cold. It is at least clear that the factors governing the occurrence of southern species in north-west Europe are very complex, and that no single simple explanation can account for them.

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IMPROVEMENTS IN THE INTERPRETATION OF RECAPTURE DATA

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1. INTRODUCTION

It is usually possible to estimate the size of human populations and communities of sessile organisms such as plants by using methods which involve fixed sampling units. On the other hand, with mobile individuals such as animals different procedures are required. One of the most widely known techniques is the use of recapture data. Records showing the proportions of marked animals recaptured seem to have been first employed by C. G. J. Petersen as early as 1889 in the study of the growth and migration of fish. Subsequently (1894 and later) he derived estimates of mortality from such data. However, Petersen's method of estimating relative abundance from length-frequency graphs did not provide values of the *total* population size. So far as I am aware, the application of recapture data for such a purpose was first made by Lincoln (1930). He estimated the total number of duck in North America, and the formula he used is sometimes called the 'Lincoln Index'. The principle is simple. A number of animals are captured, marked and released. When the marked animals are thought to have mingled thoroughly with the unmarked, a further sample is captured and the proportion of marked individuals noted. Then an estimate of the total population size is given by dividing the number of marked animals released by the proportion found to be marked in the second group of captures. Jackson (1933) independently used the same method for estimating the density of tsetse flies. In a subsequent extension (Jackson, 1937, 1939) he used his 'negative' and 'positive' methods to allow for the complication introduced by birth- and death-rates. Later work by Jackson (1940) discusses the effect of migration. Dowdeswell, Fisher & Ford (1940, 1949) have applied recapture methods to Lepidoptera populations, catching, marking and releasing moths on several different days. This kind of data can be set out in triangular arrays—the well-known 'trellis diagrams'. Fisher & Ford (1947), in their discussion of trellis diagrams, showed how to estimate daily numbers, taking into account a death-rate obtained from the average time interval between the release and recapture of marked specimens. The published papers referred to above have been largely concerned with *estimates* of population size, and of birth- and death-rates; there has been little discussion of the *precision* of these estimates. Jackson (1937, 1939) did give some attention to the latter problem but his method of fitting curves to series of 'standardized' recapture rates is not entirely satisfactory owing to absence of proper weighting factors. Although Schnabel (1938) considered the maximum-likelihood estimation of the total number of fish in a lake using data for repeated sampling, she gave no discussion of the relevant precisions. Schumacher & Eschmeyer (1943) have used a somewhat different method of analysis, but this has the disadvantage of not leading to efficient estimates, although their standard errors can be calculated. More recently,

Gilmour, Waterhouse & McIntyre (1946) have made an ingenious study of the population density of the sheep blowfly with a combination of recapture data and random walk theory. The review paper by Ricker (1945), which discusses some applications of recapture methods to fishery problems, is perhaps also worth mentioning. A fairly elaborate mathematical treatment of the estimation of death-rates alone from recapture material has been given by Leslie & Chitty (1951). In another recent paper (Bailey 1951) I examined both the bias and precision of the usual estimate of population size for simple recapture, and suggested some modifications to improve estimates from small samples. Maximum-likelihood treatments of Jackson's 'positive' and 'negative' methods, involving birth- and death-rates as well as population sizes, were also given. There was in addition some discussion of trellis diagrams, and particular attention was drawn to the simplification introduced by using the 'triple-catch' method, which involves the simple trellis diagram obtained where catching is confined to three occasions only.

The purpose of the present discussion is to give an elementary account of the results obtained in my 1951 paper, to which the reader may refer for the detailed mathematical analysis and for a description of some of the more complicated applications. A few new results are also given, with an indication of the method of derivation. These comprise the special cases of Jackson's 'positive' and 'negative' methods when catching occurs on only three occasions. It will be assumed that the reader is familiar with the simple ideas involved in considering estimates of unknown quantities, together with their bias and variance (or the latter's square root, the standard error). Thus if an estimate, of population size, for example, is biased, this means that in the repeated use of such an estimate it will be on average too high or too low, according to whether the bias is positive or negative. It is desirable where possible to employ estimates which are unbiased or nearly so. The standard error is a measure of the accuracy of the estimate to which it is attached. In large samples at any rate, when the estimate obtained by maximum likelihood will be approximately normally distributed, there will be roughly one chance in three that the true population size lies outside a range of one standard error on each side of the estimate obtained; or about one chance in twenty that the true value is more than two standard errors away.

The formulae given require no more than arithmetical substitution for the various algebraic symbols. In the general case of Jackson's 'positive' method maximum-likelihood estimation necessitates the use of scores and information functions, for an account of which reference should be made to my 1951 paper.

It is further assumed in the present elementary treatment that animals are selected at random from the population; and that marked animals have the same birth- and death-rates, and are equally likely to be caught, as the unmarked. Whether these assumptions are justified in any particular case is for the investigator concerned to decide by the light of experience. The more complicated situation occurring when there are important differences of behaviour between marked and unmarked animals requires a more complex analysis beyond the scope of the present paper.

2. SIMPLE RECAPTURE

(*a*) *Direct sampling*

In simple recapture we catch, mark and then release a animals from a total population of size x. When these marked animals have freely mixed with the unmarked we catch a further sample of size n, of which r are found to be marked. The problem is to find a satisfactory estimate of x, together with its precision in terms of a, r and n. We assume that there is no emergence of new unmarked animals and that any death-rate which operates affects marked and unmarked animals in the same way (although the latter may hold for large numbers it is unlikely to be true for small ones). In the present subsection we are considering *direct* sampling, that is the standard errors are calculated with respect to repeated sampling for which the number of animals caught on the second occasion, n, remains constant. In practice this condition may be very closely fulfilled, even if not exactly. For example, we may decide beforehand to catch 50 animals on the second occasion, but in the event it may be easy to capture the first 45 but prohibitively difficult to obtain all the remaining 5 in the time available. The alternative procedure of *indirect* sampling will be considered in the following subsection.

Now the ordinary maximum-likelihood estimate of x is

$$\hat{x} = an/r, \tag{1}$$

with variance

$$\text{var}\,\hat{x} = a^2 n(n-r)/r^3. \tag{2}$$

These formulae are quite satisfactory for samples which are large enough for the average value of r to be fairly large. For if we write

$$m = Er = an/x, \quad \text{where } E \text{ represents the expectation or average,}$$

then, omitting samples for which $r = 0$, it can be shown the estimate $\hat{x}$ has a positive bias of order m^{-1}. Thus suppose $x = 1000$, and $n = a = 100$. Then $m = 10$, and although we catch as many as 100 animals the average relative bias is as high as $10\,\%$.

A better estimate to use is one obtained by a slight modification of $\hat{x}$:

$$\check{x} = a(n+1)/(r+1). \tag{3}$$

The bias of $\check{x}$ is of order e^{-m}, which is quite small even for moderate m. In the example given above, the relative bias is less than $2{\cdot}5 \times 10^{-5}$. In large samples, of course, $\check{x}$ approximates to the maximum-likelihood estimate $\hat{x}$, given in (1). An exact value for the variance of $\check{x}$ in terms of x, a and n is not available, but a nearly unbiased estimate of var $\check{x}$ can be obtained and is quite satisfactory in practice. If we put

$$V = a^2(n+1)(n-r)/(r+1)^2(r+2), \tag{4}$$

then we can use V as an estimate of var $\check{x}$. The relative bias is of order $m^2 e^{-m}$, which in the example above is only $2{\cdot}5 \times 10^{-3}$.

In some ecological problems it may be convenient, or even more appropriate, to use the reciprocal of population size, $y = x^{-1}$. The maximum-likelihood estimate of y is unbiased and gives no trouble. We have

$$\left.\begin{aligned} \hat{y} &= r/an, \\ \text{var}\,\hat{y} &= y(1-ay)/an. \end{aligned}\right\} \tag{5}$$

(*b*) *Inverse sampling*

As an alternative to *direct* sampling we may consider *inverse* sampling. With this method, instead of aiming to catch a predetermined total number of animals on the second occasion, we continue catching until we have a predetermined number of marked animals. This procedure is not always possible in practice, but when it is it very conveniently leads to an unbiased estimate of x, and an exact value of the variance, both of which are valid for any size of sample, however small. We have the estimate

$$x' = \frac{n(a+1)}{m} - 1, \tag{6}$$

with variance

$$\text{var } x' = (a-m+1)(x+1)(x-a)/m(a+2). \tag{7}$$

3. JACKSON'S 'NEGATIVE' METHOD

The principle of the 'negative' method (Jackson 1937) is that we catch, mark and release groups of animals on several successive occasions, making no record of the numbers of *recaptures* until the last occasion. Such a method is suitable when the preliminary marking of successive batches can be carried out by relatively unskilled workers. Careful classification of animals according to the number of marks they bear is then required only on the final occasion.

Suppose that on the jth day previous to the last day a_j freshly marked animals are released. Then if there is a constant death-rate γ, this means that $a_j e^{-\gamma j}$ will survive to stand a chance of recapture on the final day. Let us catch n animals altogether on this occasion, of which r_j were first marked on the jth day previously, while r_0 are unmarked. A few animals may have been marked more than once. Although we shall lose a small amount of information it is convenient to take notice of the earliest mark only. Let x be the size of the population on the last day. In addition to estimating x, we have to estimate γ as well, or, what is perhaps a little simpler, ν, where

$$\nu = e^{-\gamma} \quad \text{and} \quad \gamma = -\log_e \nu. \tag{8}$$

Let us write

$$A = \sum_{j=1} j r_j, \tag{9}$$

and

$$c_j = a_j\left(j - \frac{A}{n-r_0}\right). \tag{10}$$

We can now obtain maximum-likelihood estimates of x and ν as follows. First we solve the equation

$$\sum_{j=1} c_j \nu^j = 0, \tag{11}$$

to give the maximum-likelihood estimate $\hat{\nu}$. This is most easily done in practice by the usual sort of iterative procedure, for which one of the standard text-books may be consulted (e.g. Whittaker & Robinson 1944). If we now write

$$\left.\begin{aligned} F(\nu) &= \sum_{j=1} a_j \nu^j, \\ F'(\nu) &= -\sum_{j=1} j a_j \nu^j, \\ F''(\nu) &= \sum_{j=1} j^2 a_j \nu^j, \end{aligned}\right\} \tag{12}$$

then the maximum-likelihood estimate of x is

$$\hat{x} = nF(\hat{\nu})/(n - r_0). \tag{13}$$

The corresponding variances are

$$\left.\begin{aligned} &\text{var } \hat{x} = (x^2/n)\,[\{xF''/(FF'' - F'^2)\} - 1], \\ \text{and} \quad &\text{var } \hat{\nu} = \nu^2 xF/n\,(FF'' - F'^2). \end{aligned}\right\} \tag{14}$$

We can find, if desired, the corresponding value of $\hat{\gamma}$ from Equation (8), the variance of $\hat{\gamma}$ being given by

$$\text{var } \hat{\gamma} = (d\gamma/d\nu)^2 \text{ var } \hat{\nu} = xF/n\,(FF'' - F'^2). \tag{15}$$

It should be noticed that the foregoing treatment is unaffected by the birth or emergence of new, unmarked individuals. This analysis of the general case of Jackson's negative method may be a little too complicated for those who are not very mathematically inclined, but for a worked example reference may be made to my 1951 paper.

If the release of marked animals is confined to only two or three occasions before the last, then the analysis can be somewhat simplified as the solution of (11) becomes very much easier. It is perhaps worth giving the results for one special case, namely, when animals are released on two occasions only, $2p$ and p days before the final day. Suppose that the numbers of marked animals released on these days are a_{2p} and a_p, and that the numbers caught on the last day are r_{2p} and r_p, respectively. Then, applying the previous results we eventually obtain the estimates

$$\left.\begin{aligned} &\hat{\nu} = (a_p r_{2p}/a_{2p} r_p)^{1/p}, \\ \text{and} \quad &\hat{x} = n a_p^2 r_{2p}/a_{2p} r_p^2, \end{aligned}\right\} \tag{16}$$

together with the large sample variances

$$\left.\begin{aligned} &\text{var } \hat{\nu} = \frac{\nu^2}{p^2}\left(\frac{1}{r_{2p}} + \frac{1}{r_p}\right), \\ \text{and} \quad &\text{var } \hat{x} = x^2\left(\frac{4}{r_p} + \frac{1}{r_{2p}} - \frac{1}{n}\right). \end{aligned}\right\} \tag{17}$$

These maximum-likelihood estimates are of course valid for large samples. For only moderate values of n we can, as in § 2, use an improved modified estimate of x:

$$\check{x} = (n+1)\, a_p^2 r_{2p}/a_{2p}\,(r_p + 1)\,(r_p + 2), \tag{18}$$

which is approximately unbiased. As before, no exact population value of the variance of $\check{x}$ is available, but we can use the quantity V, where

$$V = \hat{x}^2 - \frac{a_p^4\,(n+1)\,(n+2)\,r_{2p}\,(r_{2p} - 1)}{a_{2p}^2\,(r_p + 1)\,(r_p + 2)\,(r_p + 3)\,(r_p + 4)}, \tag{19}$$

which is an approximately unbiased estimate of var $\check{x}$.

4. JACKSON'S 'POSITIVE' METHOD

The principle of the 'positive' method (Jackson 1937) is, in contrast to the 'negative' method, to release a large number of marked animals on a single occasion. Catching then takes place on a number of later occasions, the number of marked animals being recorded each time. The majority of animals captured on these latter occasions should be released again, otherwise we should have to take special account of the diminution

in the number of marked animals available for recapture. A death-rate which applies to marked and unmarked animals equally will not affect our analysis, and may be ignored, but allowance must be made for the existence of a birth-rate β. Suppose that the population is initially of size x, of which a animals are marked. After j days there will be $xe^{\beta j}$ animals altogether, of which a will be marked. On the jth day let us catch n_j animals, r_j of which bear marks.

Now the maximum-likelihood treatment of the general case of the 'positive' method is more difficult than that of the negative method, as it does not lead to such easily solved equations as (11) and (13). We have, in fact, to adopt the method of using maximum-likelihood scores and information functions. An account of this procedure is beyond the scope of the present treatment, but those who are prepared to undertake such an analysis should consult my 1951 paper (p. 300).

However, in a manner somewhat analogous to that occurring in the 'negative' method, simplified formulae are available when catching is confined to two subsequent occasions only, p and $2p$ days after the first, respectively. It can be shown that the maximum-likelihood estimates of x and $\rho = e^{\beta}$ are

$$\left.\begin{aligned} \hat{\rho} = e^{\hat{\beta}} &= (r_p n_{2p}/r_{2p} n_p)^{1/p}, \\ \text{and} \quad \hat{x} &= a n_p^2 r_{2p}/n_{2p} r_p^2, \end{aligned}\right\} \tag{20}$$

together with variances

$$\left.\begin{aligned} \operatorname{var} \hat{\rho} &= \frac{\rho^2}{p}\left(\frac{1}{r_p} + \frac{1}{r_{2p}}\right), \\ \text{and} \quad \operatorname{var} \hat{x} &= x^2\left(\frac{4}{r_p} + \frac{1}{r_{2p}} - \frac{4}{n_p} - \frac{1}{n_{2p}}\right). \end{aligned}\right\} \tag{21}$$

As with the 'negative' method we can use the modified estimate of $\hat{x}$

$$\breve{x} = a(n_p + 1)(n_p + 2) r_{2p}/n_{2p}(r_p + 1)(r_p + 2), \tag{22}$$

which is approximately unbiased even for only moderate values of n_p and n_{2p}. An approximately unbiased estimate of the variance of $\breve{x}$ is

$$V = \breve{x}^2 - \frac{a^2(n_p + 1)(n_p + 2)(n_p + 3)(n_p + 4) r_{2p}(r_{2p} - 1)}{n_{2p}(n_{2p} - 1)(r_p + 1)(r_p + 2)(r_p + 3)(r_p + 4)}. \tag{23}$$

5. TRELLIS DIAGRAMS

Jackson's 'negative' and 'positive' methods are really only special cases of a more general situation in which the majority of animals captured on a particular day are released again, while all captured specimens are examined on every occasion for evidence of previous marking. As before, it is convenient to take notice of the earliest mark only, when there is more than one. The complete data showing the numbers of captures, releases and recaptures can be exhibited as a triangular array or 'trellis' diagram. Fisher & Ford (1947) have used a method of analysing such arrays, which allows one to take into account a death-rate which is estimated from the average time interval between release and recapture. Daily estimates of population size can then be calculated, though it is unfortunately difficult to know what precision to attach to the results thus obtained.

The triple-catch method

The general treatment of a large trellis diagram presents considerable difficulty, but if we confine our attention to catching on 3 days only it is possible to obtain fairly simple estimates of population size, and birth- and death-rates. Suppose that on the first day we release s_1 marked animals. On the second day we catch n_2 animals, of which n_{21} were marked on the first day and n_{20} are unmarked; s_2 freshly marked animals are released. On the third and final day n_3 animals are caught, of which n_{31} were marked on the first day, n_{32} were first marked on the second day and n_{30} are unmarked. Let the population size on the second day be x. Suppose that the time intervals between the first and second days, and between the second and third days, are respectively t_1 and t_2. Birth- and death-rates are β and γ, with $\rho = e^{\beta}$ and $\nu = e^{-\gamma}$, as before. Application of the method of maximum-likelihood leads to the estimates

$$\left.\begin{aligned} \hat{\rho} &= (n_{21}n_3/n_2n_{31})^{1/t_2}, \\ \hat{\nu} &= (s_2n_{31}/s_1n_{32})^{1/t_1}, \\ \text{and} \quad \hat{x} &= s_2n_2n_{31}/n_{21}n_{32}. \end{aligned}\right\} \tag{24}$$

The corresponding large-sample variances are

$$\left.\begin{aligned} \operatorname{var}\hat{\rho} &= \frac{\rho^2}{t_2^2}\left(\frac{1}{n_{21}}+\frac{1}{n_{31}}-\frac{1}{n_2}-\frac{1}{n_3}\right), \\ \operatorname{var}\hat{\nu} &= \frac{\nu^2}{t_1^2}\left(\frac{1}{n_{32}}+\frac{1}{n_{31}}\right), \\ \text{and} \quad \operatorname{var}\hat{x} &= x^2\left(\frac{1}{n_{21}}+\frac{1}{n_{32}}+\frac{1}{n_{31}}-\frac{1}{n_2}\right). \end{aligned}\right\} \tag{25}$$

For data in which n_{21}, n_{32} and n_{31} are only moderate there is some advantage in using the approximately unbiased estimate

$$\breve{x} = \frac{s_2(n_2+1)\,n_{31}}{(n_{21}+1)\,(n_{32}+1)}, \tag{26}$$

for which we may use the approximately unbiased estimate of variance

$$V = \breve{x}^2 - \frac{s_2^2(n_2+1)\,(n_2+2)\,n_{31}(n_{31}-1)}{(n_{21}+1)\,(n_{21}+2)\,(n_{32}+1)\,(n_{32}+2)}. \tag{27}$$

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FLUCTUATIONS IN THE NUMBERS OF BRITISH TETRAONIDS

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(With 4 Figures in the Text)

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INTRODUCTION

By the courtesy of the owners and factors, I have been able to get grouse bags for varying periods from many game books. These are treasured personal possessions and my very sincere thanks are due to my correspondents, without whose co-operation little could have been done. The British red grouse (*Lagopus scoticus* (Lath)) called 'grouse' in this paper, is reputed to have a cycle of 7 years, and game-book records of bags distributed over the whole range have been collected to see to what extent such fluctuations occur and their time and space relations *inter se*. At the same time data were collected for the other three British tetraonids, the capercailzie (*Tetrao urogallus* L.), the black grouse or blackgame (*Lyrurus tetrix* L.) and the ptarmigan (*Lagopus mutus* (Montin)). It proved more difficult to get satisfactory figures for these species than for grouse, and the numbers everywhere were much smaller. The main figures came from central Scotland, Perth and Angus, with blackgame from eight big shoots in south Scotland for comparison.

The game-book data cover a long period, some back to the 1830's and many to the fifties. The figures are those of birds shot and not of populations. A low number or zero does not mean that the population is nil as low stocks are conserved, but on a 10,000-acre moor the stock was said to be four birds the year after the bag had been 3402 (Committee of Inquiry on Grouse Disease 1912, p. 443). When stocks are very big it is unlikely that the whole shootable surplus is killed as the birds get wild and

pack. So in the best and worst years the bag may be lower than usual in comparison with the population.

Game books are written up by numbers of different people giving figures from actual returns with no special theories in view. The bags themselves are accurately counted, which eliminates errors of estimation. Apart from being relatively low at the two extremes of density, the numbers of birds shot may be affected by the weather, by the skill of guns and dogs and on a leased moor by the limit set to the bag. But this limit may not be reached, and in a good year the owner may have a few days shooting after the lease expires. A good manager, whether owner or keeper, has a good idea of the birds left and controls numbers by the number of days' shooting and even by deliberately working a moor in such a way as to preserve stocks, which may be wrongly considered bad driving. Failure to let a moor may result in a poor bag as may the death of the owner or lessee, but with the number of moors in the present sample this is not important and can generally be seen from notes. Good moors are expensive both to lease and to maintain, and the income from them is such that steps are taken to get them properly shot except in national upheavals such as the two world wars. So bags give a fairly reliable index of numbers as a whole, and as will be seen the fluctuations are so great that even allowing for a considerable error, years of abundance and scarcity are still obvious.

The terms 'good' and 'bad' years have been used. These are not necessarily the same as peaks and crashes as there may be two good years running. A good grouse year is a year when bags are big. A good year for grouse may be different as if the breeding stock is low, the bag is also low as stocks are conserved. In practice, the proportion of old to young birds in the bag is a good test; when this is one to two, it is a good year for grouse, and when it is one to one or lower, a bad one. The number of barren pairs and single birds seen is also a criterion. In old records, the ultimate test is the size of the bag. 'Overcrowding' is used as a convenient term when the density is too great for the resources of the habitat, but it implies considerable numbers. A limiting factor may come into action at a low population level and prevent numbers from reaching the stage at which this term can properly be applied, although the principle is the same. With grouse, overcrowding may mean a bird to an acre under optimum conditions, but in the west of Scotland, the Hebrides and Ireland the same condition is reached at a much lower density, of the order of one bird to 50 acres. 'Critical density' is a more formal term for the stage above which numbers are too great for the available resources, the 'carrying capacity' of Americans.

POPULATION DATA

(*a*) *Grouping of moors*

A 'moor' is thought to be the real unit, but it is an elastic term and may cover any area from 100 acres upwards. One known to me covers 30,000 acres, including several villages, but is spoken of as 'the moor' or 'the low ground' as opposed to the deer forest. The term is used loosely, not meaning a definite number of shooting units (beats) or records. To give acreage creates a false impression as optimum density varies from 3 to 100 acres or even more per breeding pair. 'Moors' in this paper mean

the smallest units for which I have been able to get data and vary in size from 500 to 30,000 acres, each unit being however compact.

Many owners have given me their figures with the stipulation that they should not be made public in recognizable form. Moors are therefore grouped into arbitrary districts. None have been left out because they do not fit in, the only omissions being those with frequent changes in area or big blanks in the records. These have been used as checks and show general agreement with the rest. The moors given are not of equal size or productivity, and an effort has been made to obtain data from those with high, medium and low densities. The approximate maximum area for each district is given at the end of the Appendix. Bags are for different periods, but the gain or loss of a moor is indicated, and changes have been made so that the additions and omissions do not of themselves create peaks and troughs. The method is not entirely satisfactory, but figures for some eighty moors are an unwieldy mass.

The actual areas concerned for other species cannot be worked out with any accuracy owing to overlap and the way in which habitat patches are scattered. As a rough approximation only for the sample, caper and ptarmigan cover about 20,000 acres each and blackgame 30,000 in central Scotland. In south Scotland, grouse moor amounts to about 100,000 acres, on most of which blackgame occur at times; the scrub and woods here cover about 10,000 to 20,000 acres. In central Scotland, ptarmigan cover 12 shoots, caper 15 and blackgame 20. In south Scotland blackgame are from 8 shoots. So the number of units for each species is considerable, as well as total birds and total area, although again the size and productive potential varies widely, which is unavoidable as I have to take the available data as I find them. For details, the other tetraonids from central Scotland should be compared with grouse from Atholl, and perhaps central Scotland, and blackgame from south Scotland with grouse from that district. Peak years for individual shoots are not given as they only show the same variation as has already been seen in grouse. There is no over-all peak year, but the available totals show definite peaks, meaning that the different shoots do not cancel each other out.

(*b*) *Definition of a peak*

Years of maximal bags have been taken as peaks, but peak levels may be maintained for two or more years, although the usual form of the curve is saw-toothed, a single year of high numbers being followed by a considerable drop with comparatively slow recovery. The operative date especially for comparison between different moors and districts may be the last year of peak abundance, when a high level gives place to a low one. This year, while obvious in most cases, is difficult to define exactly; it is the year before the crash, a sharp and heavy decline in numbers, but a peak is not invariably followed by a crash. Data have been worked out by both methods and the difference in the general picture is not great. The total number of grouse units with maximal peaks in each year is given in the Appendix.

(*c*) *Local fluctuations*

This investigation started after seeing the figures for the Atholl Estates, Blair Atholl, where records are available from 1866 onwards. Up to 1931 they cover roughly 100,000 acres and there are totals both for the whole estate and for the twenty-one

individual moors which comprise it. From 1927 onwards several moors were sold or afforested, so figures from that date are for a progressively smaller area. With full data for 66 years and the records all kept in one office, this provides an admirable datum line. Graphs for four moors are selected to show variation combined with general agreement up to the early 1940's (Fig. 1). With central administration, the standards of management are much the same and improvements spread quickly. An estate pool of labour helps to keep conditions at the same level, so it is probable that any differences are inherent in the habitats and not due to human interference. The bag varied between about 2500 and 28,000 birds, the general average being about 13,500; the size of the sample smooths the curve.

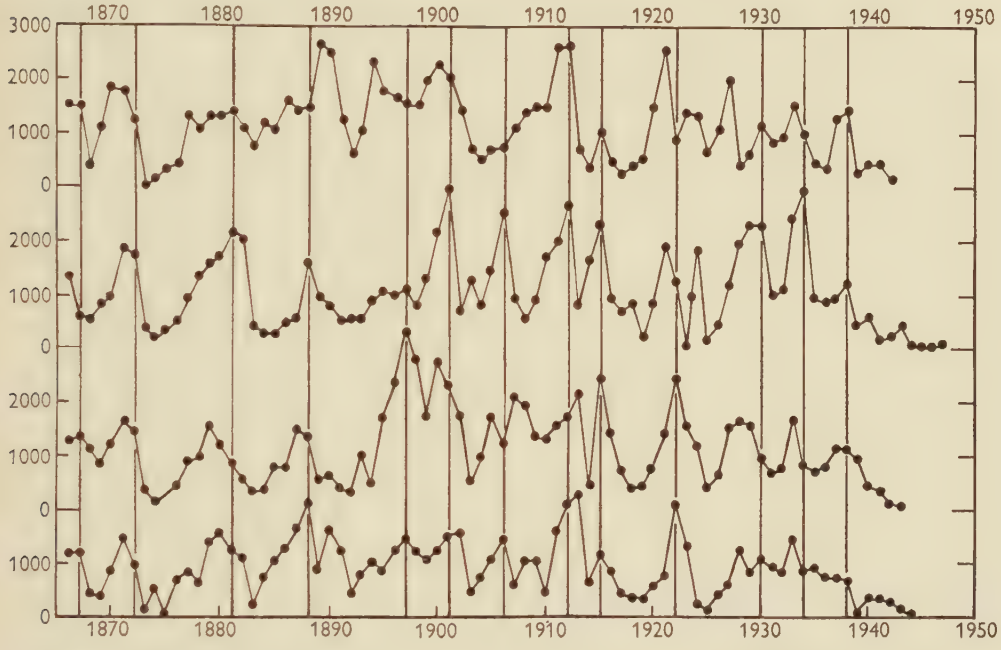

Fig. 1. Individual variations in the numbers of grouse shot on four moors of the Atholl Estate. Vertical lines show peak years for the estate as a whole.

From 1866 to 1941 there were 14 peaks, or 13 periods. There were two doubtful years, 1897 and 1915, discussed below. This gives an average period of 5·9 years. If 1897 and 1915 are both omitted, the average becomes 6·9 years, and if 1915 only is omitted, 6·4 years. These averages and those below are given but are not thought to be of exact significance. This is because the whole fluctuation depends on the interaction between the species and many factors: rainfall and humidity, temperature including sunshine and frost, snowfall and wind, food supplies especially various fruits and seeds, predation which is mainly but not entirely shooting, buffer species, burning and re-growth, and drainage, always modified by their incidence on a particular moor, the lie of the land. There are so many complications, including that of deciding which is a peak year, that it can usefully be said only that the period varies from 3 to 10 years.

Fig. 1 shows that peaks often vary by 2 years either way, e.g. 1906–7, 1887–9. The effect of this on the total is to reduce both the drops and the peaks as one or two moors

may be early or late. There are some pairs of years when nearly all moors had good bags followed by crashes: 1866–7, 1871–2, 1906–7, 1912–13. There are other times when all moors had peaks with the ensuing crash, but the actual peak year varied by as much as 4 years, e.g. 1894–7. This also appears in the district figures and we return to it later. Considerations of space make it impossible to give all data in detail, but between 1894 and 1898 nearly all moors had peaks or showed a change in conditions. Some crashes were big, and one moor had its record year in 1897. This flattens the curve in the total, but from consideration of the individual moors, it is clear that there was a peak at about this time, but that it was spread out over a number of years in different places. This is confirmed in other districts, and 1897 is allowed as a peak.

1915 is different. There was a very big peak only 3 years after the 1912 one, which was generally a record year. The first World War, starting in 1914, led to shooting arrangements being abandoned, so bags were small. In 1913 there was a crash, but from the size of the bag the term was only relative; numbers were nearly up to the level of previous peaks, having been exceeded only twice, in 1901 and 1906. The interruption or prevention of shooting in 1914 gave a chance of recovery which allowed stocks to improve greatly in 1915. Three years is too short an interval to allow for an ordinary crash and recovery. But 1910 was the peak in the Outer Hebrides and on some English moors, while others were in 1911, which would make 1915 within the normal recovery period.

I have not been able to connect crashes or peaks with any one climatic event such as heavy snow or rain, which is perhaps not surprising as the years differ even in a comparatively small area of 100,000 acres. Notes in game books are put in after the season to account for a bad bag and so lose much of their value. They are in any case often conflicting, one moor noting heavy snow or rain and another nearby a good season or no remarks. The only consistent difference seems to be the moors themselves, their height, exposure and wetness. With drifting snow some moors are worse off than others according to the wind and altitude, and a very wet year may be good on a dry moor and vice versa. The same weather affects different moors in different ways.

The course of events on the Atholl moors can be seen from the Appendix. The actual figures for the various moors are not thought to be essential for understanding the problem, as they only show on a smaller scale what is shown by the figures for the range as a whole. The grouse figures for central Scotland follow those of Atholl fairly closely. But the agreement is not exact (1895–7, 1921–4), the difference being of the same order as in Fig. 1 for Atholl moors. 'Peak periods', to which we return later, are indicated, periods of 2–4 years during which most peaks on individual moors occur. Figures for the other tetraonids for central Scotland are given in the Appendix, and their peaks, with those of the grouse total are shown in Fig. 2. It is convenient to take grouse as standard as they are the biggest single group of data and we have a general picture for the whole country for reference.

The peak periods suggested for grouse reflect differences in the effect of conditions on a single species. A peak consists essentially of two phases: a build up in good or normal conditions to produce high numbers, making the population vulnerable, and a crash either associated with bad conditions which may last for one year only, or because gross overcrowding itself creates unfavourable conditions. For the four

species living in the same general locality, peak periods are slightly different from those for grouse over the whole country. They were first taken to be the grouse peak year plus the years before and after it, but this does not allow for the variation in the effect of any condition on grouse on different moors, as well as on different species. Just as other species may be a year early or late with reference to the 'normal' peak year, so also may grouse. To allow for this the general peak period for all species is taken as any two or three years including the grouse peak. They have been marked with a line on the left of the years in the Appendix. It will be seen that they do not coincide with the peak periods for grouse all over the country, the line on the right of the year, but they always overlap and show a close connexion. Grouse data cover one species over a wide area, while here we are dealing with four species over a relatively small one.

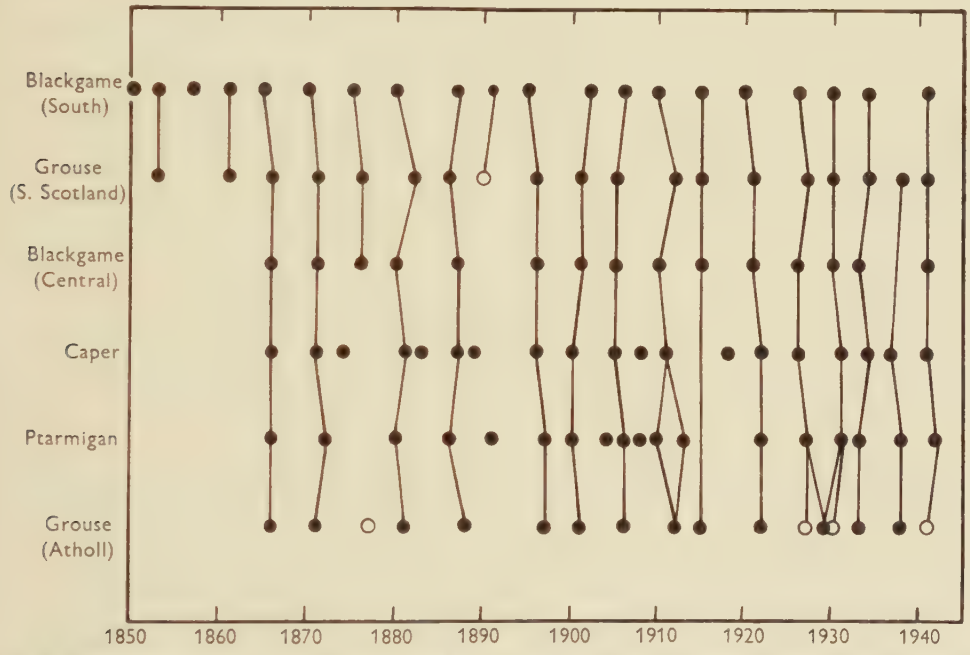

Fig. 2. Peak years for tetraonids in central and south Scotland linked to show suggested time relationship. Hollow circle, 1929—Atholl grouse had a peak in 1929, but this was abnormal, 1927 and 1930–31 being the normal years. See Appendix.

Moran (1952) deals with the statistical aspects of correlation between the four species in central Scotland, using a set of figures for the other three species which I have been able to increase a little since sending them to him, and grouse figures for a restricted area in which Atholl was the major moiety. Figures for south Scotland were only obtained recently and are not included. I am not competent to discuss his findings but, shortly, he says that grouse, caper and ptarmigan fluctuations are all definitely related, while blackgame, although related to grouse, do not show a connexion with caper or ptarmigan. It is possible that the higher figures from south Scotland may modify this. He says that the evidence of correlation is statistically strong, which enables his method to be used. Moran's paper is of primary importance on the question of correlation. He deals with rises and falls; it is perhaps permissible

to discuss shortly peak years, an aspect of the figures which is more obvious to one who is not a statistician, without in any way questioning his findings or methods.

Years of maximal bags and years before crashes are usually but not always the same, because the typical peak is sharp. Duplicate peaks occur in all species, being clearer in small units than in big groups, and occurring more frequently in caper and ptarmigan, in which habitat niches are restricted and density low. It is difficult to understand them unless they are produced by overshooting or a year when breeding stock is high but conditions are bad for young birds but not for old ones; for instance, destruction of nests and eggs or shortage of insect food such as has been shown to have an adverse effect on the survival of nestling tits (Mackenzie, 1950). If it were the latter, old birds should form a high proportion of the bag in the intervening bad year; while there are some indications of this from notes, they do not amount to proof.

Table 1. *Other tetraonid peaks as related to grouse peaks in the same district*

	Central Scotland, 1866–1941			S. Scotland, 1850–1941	
	Ptarmigan	Caper	Blackgame	Blackgame	Total
−2 years	2	.	1	2	5
−1 year	2	7	7	6	22
Same year	7	4	6	6	23
+1 year	3	3	.	4	10
+2 years	1	2	.	.	3
Other peaks	1	3	1	2	7
No peak	2	1	1	1	5
Total	18	20	16	21	75

Note. Atholl peaks have been modified to conform with the general picture, 1877 being taken as a peak and 1929 replaced by the normal years, 1927 and 1930. This represents more nearly the situation in the area from which the other species come.

Grouse, the standard species, fluctuate in loose general agreement throughout the British Isles. The period is not regular, but also not absolutely irregular. The figures for the other tetraonids show the same features, and correlation is usually best with grouse in the same district. Table 1 shows the numbers of peaks in each species and their time relationship to the Atholl grouse peaks. To give as complete a picture as possible, blackgame in south Scotland, referred to below, are included here also, the comparison being with grouse in south Scotland. Of 75 actual and potential peaks, five were missed; ptarmigan in 1877 and 1915, caper in 1915, and blackgame in central and south Scotland in 1938. These dates were subject to war influence, and a peak may sometimes be missed out even with the high numbers in grouse, e.g. Wales 1915. The seven 'other' peaks were ptarmigan 1891, caper 1874, 1918 and 1941, blackgame central 1941, and blackgame south 1850 and 1857. In 1891 blackgame south had their peak, with one of a series of three duplicate peaks in south Scotland grouse in 1890: the grouse moors directly associated with these blackgame had their peak in 1890 and not 1886–8. The caper peak in 1918 was due to one unit in which woods were being felled, the bag being mainly the breeding stock. Caper and blackgame 1941 peaks were in the year of a small but general grouse peak. The bag in 1874 is related to the 1876–7 peak. Blackgame peaks occurred in the south in 1850 and 1857 when data were meagre; there was a grouse peak in Wales and Ireland in 1857 and there are some other indefinite indications that these years were good, such as a note in *The*

Scotsman of 5 September 1851 saying grouse and white hares were plentiful but blackgame scarce (as they would be after a crash): '(Blackgame) is giving way rapidly before the grouse.' So there are reasons for those peaks which seem to be out of step. There is also a tendency shown for blackgame and caper peaks to be before rather than after those of grouse, 27 being before and 13 after.

Differences in the average interval between peaks are not due to a general change in the length of the period but to the interpolation of extra peaks, e.g. ptarmigan 1900–04–06–08–13. These interpolations often occur when the interval between grouse peaks is long, 1857 and the 1876 group, but in south-Scotland grouse there are three duplicate peaks in 1886–88–90. A possible explanation is that ptarmigan and caper, with their restricted and confined habitat niches and lower densities, tend to reach a peak more quickly than grouse and, to some extent, than blackgame. This might also be why their peaks are before rather than after grouse, and why duplicate peaks occur. Caper and ptarmigan may show a greater or quicker power of recovery, partly because they are not subject to strongylosis with its extreme reduction in numbers and lowered vitality. See Moran (1949) for an analysis of the lynx and sun-spot cycles, where the change is gradual and due to a slight difference in the periods.

It is normal for all the tetraonids in a given area to have their peaks in peak periods of 2 or 3 years. The troughs between peaks average about 3 years. It is extremely unlikely that this will happen on fourteen occasions by chance; the 4-year period, 1910–13, was when grouse bags were so high that they show abnormally favourable conditions which probably postponed the crash. I can see no explanation except the effects of some common factor. This might be the qualitative or quantitative value of their common food, vegetation, but I know of no proof.

(*d*) *Regional trends*

Lagopus scoticus scoticus. In other districts grouse show general agreement with the Atholl peaks, with the same variation in the actual peak year. Before 1866, even with only three units, there was variation in the actual year for moors, although the district peak is clear. The number of periods can be seen for each district. Including 1915, the total is 20 for 105 years, 1837–1941, an average of 5·3 years with variation from 3 to 10 years. If the 4 doubtful years, 1840, 1877, 1930 and 1941, are all excluded, the average becomes 6·6 years. There has been a further series of fluctuations (see below), the evidence being derived from notes of disease outbreaks; this would give 26 periods between 1797 and 1941, 145 years, an average of 5·6 years or with 22 periods only, 6·6 years again. The average from 1837 to 1888 was 5·8 years, and from 1888 to 1941, 4·9 years. This may reflect the result of improved management measures, especially after 1912, bringing the stock to a vulnerable density more quickly.

Besides the variation in moors in each district, there is also some variation between districts at some distance from each other, e.g. west Scotland, Argyll and the Isles (which are separated by a natural barrier), and England had peaks in 1911 and 1913 respectively, although 1912 was the year over the rest of Scotland.

We have figures showing peak years from 1834. Before that the Committee of Inquiry on Grouse Disease (1912) and Vesey-FitzGerald (1946) give certain years

as bad for disease in certain places from past records. These are 1797, 1803, 1809–11, 1815, 1822, (1831) and 1838. 1831 is included as a crash year by me by inference, as the figures for 1834–7 show that recovery was taking place, and it is fair to assume something from which to recover; a peak was due just about then. 1803 depends on Macdonald's statement (Committee of Inquiry on Grouse Disease 1912, p. 152): 'it is now (1883) eighty years since the alarm of Grouse Disease was sounded in this country'. This would give an outbreak in 1803 if 80 years is intended to be an exact figure; the original references are in the Grouse Committee's report, but I have not seen them myself.

The figures for each moor have been carefully examined and checked with moors not included owing to gaps etc., and those for each district represent the general position correctly as far as the samples show it. Individual moors do not follow the district curves exactly, and it is the rise and fall relative to the years before and after which are important rather than the exact figures or any change in level. Figures taken from Middleton (1934) for grouse are included in their respective districts. This gives a more complete picture than my figures alone, as satisfactory records for these localities and periods have been difficult to get. They can be found in his paper and their dates and code letters in my Appendix are: south Scotland (Lanarkshire) i, 1858–1909; north-east Scotland (Aberdeen) a, 1849–1904; west Scotland (Bute) b, 1897–1924; England east and centre (Cumberland) a, 1848–1904. The Bute figures have been extended up to 1945.

Although some years produced general peaks, for some moors these conditions were reversed. In 1906, 25 moors had peaks; yet 5 moors with peaks in 1905 crashed in 1906, the 'good' year, while in 1907 when 25 moors crashed, some very heavily, 10 moors had peaks. This indicates that density is important, yet some moors had bags of much the same size both in 1905 and 1906, and 1906 and 1907, crashing after the second year. The same thing happens at other peaks and points to the importance of local conditions.

The period 1920–31 is curious. There were two main peak periods, 1921–4 and 1927–31. During each of these several moors had two peaks. In each peak period, there were two main peak years, 1921 and 1924, and 1927 and 1930. It is possible that this is connected with recovery from the neglect during the war years, each of the two groups representing two peaks coalescing to some extent.

The numbers of moors with peaks in each year show that up till 1865 with from 3 to 11 units, there was good agreement. After 1865, with from 29 to 54 units, peak periods are still noticeable. From 1876 onwards, 1883 and 1892 are the only years with no peak up to 1944, when the influence of the war overrode everything. But the number varies from 1 to 31, from under 2 to 66% of the possible maximum. If years when less than six moors, that is 10% and under, had peaks are eliminated, we are left with a series of peak periods, each from 2 to 5, usually 3 years. Almost all peaks for districts are in these periods, as are most of the Irish and Hebridean peaks.

Lagopus scoticus hibernicus. Figures for the Outer Hebrides and Ireland are given In the former, the area shot over after 1893 was 30,000 acres, but before that date it was at least double that figure. The moor is very wet, and the decline from about 600 birds after 1908 may be connected with increasing precipitation. There is

no record of disease, and from personal knowledge the place is so well managed that an outbreak could not be missed. The Minch, 25 miles of sea, acts as a barrier to migration and so to infection from the mainland, but as far as I know, no birds have been examined in a laboratory for worms. The maximum observed density is low, yet rises and falls still persist, and occur at much the same intervals and in much the same years as on the mainland. Peak years are given in Fig. 3 for comparison with the mainland and Ireland. These areas are entirely unconnected by land, but there is a considerable degree of synchrony, although statisticians say the agreement is not close. The 1891 peak in the Hebrides was perhaps late owing to lack of shooting in 1883–5 (there were local peaks elsewhere in 1890) and the 1938 peak on the mainland was probably early owing to reduced shooting in 1939. The 1896 peak does not appear in the Hebrides, but even with adjoining moors one sometimes misses a peak found on the other, and this peak is everywhere variable. The 1912 peak appears in 1910, and this has been noted as one reason for thinking that the 1915 peak is a real one in

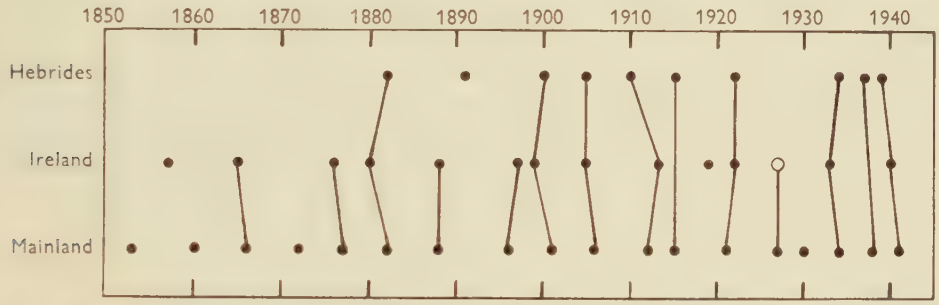

Fig. 3. Peak years for *Lagopus scoticus scoticus* and *L. s. hibernicus* linked to show suggested relationship. Hollow circle, 1927, Ireland—the total shows no peak, but every moor had a peak between 1927 and 1931. See Appendix.

spite of the war, perhaps induced earlier than it would otherwise have been on the mainland by abnormal conditions. The 1927 peak does not show in Ireland, but every moor had a peak between 1927 and 1931 which cancel each other. With no disease record, disease cannot here be related to rises and falls. Drops are locally considered to be due to bad nesting seasons, and this is probably right, although all bad nesting seasons are not necessarily followed by heavy drops.

There does not seem to be anything to show how deaths mainly from weather or other unfavourable conditions, and deaths mainly from or at least associated with disease, are connected. But a comparison of peaks in the Hebrides (and Ireland) with those on the mainland indicate that there must be some connexion.

I do not know Ireland but have been corresponding with some fifty men there. Grouse seem to be nearly, if not quite, extinct in the south, foxes and poaching being blamed. In the north, I have bags from one moor each in Co. Roscommon and Co. Dublin, and nine from Northern Ireland. The density is low generally, of the same order as that in the Outer Hebrides, but may occasionally be high. I have a note that one mountain, 283 acres, yielded 242 birds in 1872, the record year, and this would be high anywhere. I have no series of bags from this moor, but 60 seems to be an average number in a good year. Extensive inquiries have produced no record of

disease, yet there are rises and falls, and the peaks can be related to those in the main group.

Other species. For other tetraonids the only figures given outside central Scotland are those for blackgame in south Scotland. The agreement tends to be rather with the local grouse than with the generalized peaks for the whole range. The peak in 1891 follows a local grouse peak in 1890.

For blackgame I have data for seven other shoots in Scotland in Dumfries, Bute, Argyll and Sutherland. The figures are small and lack of space prevents giving them. They show the same general agreement with the local grouse peaks as those in the Appendix. Data run from 1878 to 1947, and the blackgame peaks are in 1882, 1887, 1891, 1895, 1901, 1905, 1910, 1917, 1922, 1926, 1930, 1934, 1938 and 1940. I have been unable to get any figures from England and Wales.

(*e*) *Long-period fluctuations*

So far the fluctuations dealt with have been short ones, 10 years and under. Reference to the figures for blackgame shows that the short waves are superimposed on longer waves of general abundance with a period of 30–50 years (Fig. 4). The two best peaks are 1860–70 (1876 in central Scotland) and 1910–15. There is another peak in 1933–4, but at a different level owing to curtailment of the habitat. The peak in central Scotland in 1921 is probably due to the resumption of shooting after the war. The slight difference between peaks in south and central Scotland may mean that a key

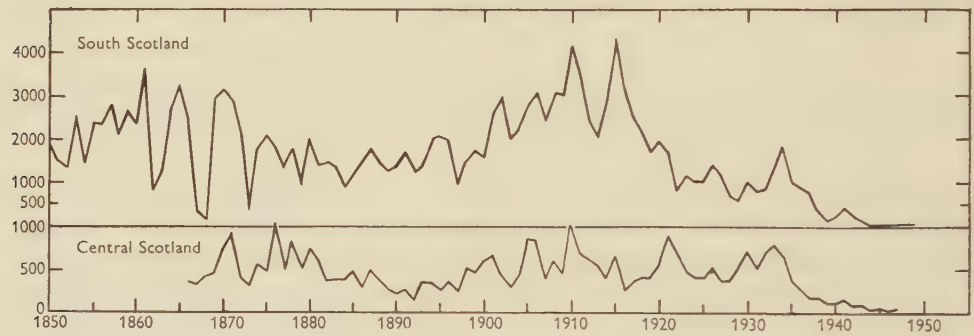

Fig. 4. Blackgame bags in central and south Scotland, to show long-term fluctuations.

factor operates differently in different places. If this long-term fluctuation is natural, numbers should be rising again now, and I have in fact reports mainly from central Scotland, that lots of from 50 to 100 birds have been seen in the last year or two, numbers which have not been approached since 1934. This may be related to Bruckner's cycle which is of about this length.

Caper and ptarmigan show no obvious signs of this fluctuation, but in grouse 1910–15 was a time of very high numbers, and peaks then and about 1860–70 are less diffuse than in the intervals in that a high proportion of moors have them in a shorter time, 2 years. 1894–7 and 1921–31 in particular are diffuse, both about the low point for blackgame.

ECOLOGICAL DATA

(*a*) *Climate*

I have only been able to examine climatic data superficially and have not found any one factor which could explain the 5–6-year fluctuations. Densities are much lower in the west than in the east and centre, which is reputedly due to greater rainfall and higher temperatures. Kalela (1949) and Watt (1950) say of the north temperate regions that temperatures have risen over the last 100 years, and that an oceanic climate has replaced a continental one. Glaciers have been receding and northern ocean temperatures have risen by 3° C. in fairly recent years: cod are being caught by Eskimos who have not even a traditional name for them. Various birds and other animals have extended their range northwards, and lakes are said to be diminishing in central Eurasia. If grouse dislike high temperatures and excessive rainfall and humidity, such changes would account for their virtual extinction in south Ireland and decrease in the Outer Hebrides and north Ireland. The east of Britain is on the dry side (moors have been improved by providing water supplies) and a slight increase in wetness to an optimum in 1910–15 would account for the rise in bags at that time. Possibly such changes (perhaps Bruckner's cycle) account for the long-term rise and fall in black-game, our race being an insular outlier of a continental species. This is, however, little more than speculation.

(*b*) *Habits*

It is not intended to go into the habits of tetraonids except for some points with a bearing on what follows. There are several excellent accounts (Darling 1947; Vesey-FitzGerald 1946; Committee of Inquiry on Grouse Disease 1912; Stephens 1939; Stuart-Wortley in Macpherson, Stuart-Wortley & Saintsbury 1894; Witherby, Jourdain, Ticehurst & Tucker 1938–41.) The grouse is a bird of the open moor where heather (*Calluna vulgaris* Salisb.) and heaths (*Erica* spp.) are the main vegetation, although it also occurs where crowberry (*Empetrum nigrum* L.) grass and rushes are found with little or no heather. When a moor is first planted up with trees, birds occur regularly until the canopy closes overhead, especially in snow and when blaeberries are ripe, although in smaller numbers than on the open moor. The altitudinal range is from 3000 ft. to sea-level.

The young can fly early, about a fortnight after hatching, and chicks feed mainly on insects at first but later the diet is almost entirely vegetable, mainly heather shoots, seeds, etc. In March and early April one finds more grouse in reedbeds and swamps than at other times of year; they are probably looking for early green shoots which appear here before the vegetation elsewhere, especially the heather, has started to grow. Until autumn they remain in family parties (coveys) which may be maintained right up to pairing time. But especially in years of abundance, packs are formed numbering up to several hundred birds, which makes it difficult to kill down the stock.

Heather is the staple food of grouse, but they eat a great variety of other things as well (Committee of Inquiry on Grouse Disease; Witherby *et al.* 1938–41). Blaeberry (*Vaccinium myrtillus* L.) shoots, fruits and buds are perhaps the most important. Where there is no heather, crowberry is said to take its place. With such a varied list

of foods, it is possible that one or other of them is essential. In a good blaeberry year, while the fruit is ripe it is little good looking for grouse except on blaeberry ground. It is likely that a shortage of fruit affects the birds by cutting out some essential food factor such as a vitamin. See Elton (1930, p. 21) for the effects of a shortage of crowberries in Labrador. See also Elton (1942). Nordhagen (1928) states that peaks and crashes of *Lagopus lagopus* L. in Scandinavia are related to good and bad years for berries, which in turn are related to climate, the late melting of snow.

Cocks may establish a territory in December, but I have never seen any real fighting then. Later they maintain a territory round the nest, and once the young are hatched the covey is usually found within a fairly well-defined area until they pack. When two coveys meet there is a certain amount of bickering, but it is not serious. The form of territory is loose and not very strictly defended, allowing outsiders to use a special food supply such as a blaeberry patch. Packs also keep to much the same area day after day, and both the covey and the pack territories are well known to keepers, who search a particular face for a particular 'lot'.

L. s. hibernicus (Kleinschm.) the Irish subspecies which is also the Outer Hebrides bird, differs from the Scottish one *L. s. scoticus* (Lath) mainly in habits. According to Witherby *et al.* (1938–41), with whom my own experience agrees, it takes shorter flights, sits more closely, follows contours rather than crossing valleys, and is inclined to use wetter ground such as peat hags. It is a shyer, less aggressive bird and I have seen little fighting even when birds are concentrated on deer tracks in frozen snow. It also uses its voice less, and the clutch of eggs is slightly smaller. I can see nothing here to account for its freedom from strongylosis, except its density which is everywhere much lower than that in most *scoticus* habitats. Owing to importations there are probably few moors to-day on which the pure *hibernicus* can be found except for a few islands.

Two or more species, rarely all four, may occur on the same shoot, but their habitats are not the same although there may be some overlap. Consequently, climatic conditions are not exactly the same although there is similarity. Caper and blackgame occur on my own small shoot near Perth, where they come for blaeberries, but they normally live in woods 1–3 miles away and at a different altitude. As a rule, each species is found mainly on its own type of ground, especially for nesting. Where all occur, caper are mainly in the older woods which are fairly low down; blackgame in the scrub and on the edges of the moor; grouse on the moor, above which is the deer forest at the top of which again lies the ptarmigan ground.

The capercailzie is found mainly in mature coniferous woods especially in winter, but since many of these were felled during the two wars, I have found woods from 20 to 30 years old being colonized, and the bird occurs in 10-year old plantations of my own. I have also found it on the open moor feeding on blaeberries, and commonly in hardwoods with scrubby undergrowth, especially near pinewoods. In winter it feeds mainly on conifer buds and shoots, but in summer the food is varied, of the same type as that of blackgame and grouse with more use of conifers. The altitudinal range is governed by that of the main habitat, coniferous woods, and runs from about 1500 ft. down to the sea. For details of distribution and re-introduction, see Pennie (1950–51) and Darling (1947). A caper cock weighs up to 12 lb. and its size, combined

with the comparative scarcity of suitable habitat, keeps numbers low. The bird finds it difficult to take wing uphill and this makes it liable to predation by foxes, etc.

Blackgame keep more to scrub than the other species, although they occur on open moors and in woods. I have found them in swamps in autumn, feeding on the seeds of sedges and rushes, and in the border country they may amount to 15 or 20% of the birds in grouse drives. Near Perth a few normally live in conifers and birch scrub, but come out on to the moor especially when the blaeberries are ripe. Its haunts tend to be wetter than those of grouse, and the food is of the same type as that of caper but with a preference for hardwood buds, mainly birch and alder. The border country seems to be the main stronghold of the species. But in matters of blackgame density the long-term rhythm referred to above must be remembered.

The Scottish ptarmigan is a bird of the high tops, in summer over 2500 ft., although in Lewis one or two coveys lived on hills under 1400 ft. up till the first World War, about 1915. I have heard of ptarmigan being shot in a high grouse drive, and I have put up grouse and ptarmigan within 100 yards of each other at the same level, so there is at times an overlap in summer and autumn. In winter they come down considerably lower, although they burrow into deep snow for food and roosting as grouse occasionally do. Their food consists almost entirely of shoots, seeds, etc., of plants found at such altitudes. The mountain tops where they live are largely barren rocks and scree. Darling (1947) gives several excellent pictures of ptarmigan country. The available food severely limits the possible density.

It will be seen that grouse overlap all the other three species, while caper and blackgame also overlap to some extent, although it is said that the two birds do not thrive in the same area, caper ousting blackgame. The densities of the other three species are usually much lower than those of grouse, although in the Borders blackgame are more numerous than elsewhere, especially in optimum years such as 1861, 1865, etc., when more blackgame than grouse were often shot. At times, in recent years, the bags here are round about a tenth of the grouse bags, a change partly due to a decrease in blackgame and partly to improved methods of grouse management. Elsewhere, bags of caper and ptarmigan are about a hundredth and blackgame about a fiftieth of the grouse bags; I think this fairly represents their relative abundance, as far as this can be done for birds living mainly in different habitats.

With their comparatively low densities and restricted habitats, caper, blackgame and ptarmigan seem to take a shorter time than grouse to rise from scarcity to a peak. It is possible that their fluctuations are more nearly analogous to those of grouse in Ireland and west Scotland, where the extreme reduction in numbers caused by strongylosis is absent or rare and density is low.

(*c*) *Management*

Ever since grouse shooting became fashionable and profitable, about 1850–60, crashes have been known and feared, and grouse disease was rather vaguely advanced as the reason for them. But it was not until 1905 that a number of proprietors initiated the Committee of Inquiry on Grouse Disease, usually known as the Grouse Committee. It concluded that strongylosis was the cause of at least some of the disasters which had befallen grouse in such years as 1867–8 and 1873. It stressed that conditions

favourable for grouse were produced by regular heather burning, drainage and shooting combined with control of numbers left for breeding. These recommendations helped, but violent fluctuations still occurred, although perhaps the peaks were higher and the crashes less severe. But the issue was clouded because in 1912 bags were the highest ever attained in the country as a whole, an effect which cannot have been due to anything initiated in 1911 only since big bags were shot on some moors in 1910. The 1914 war caused neglect of management measures and a heavy drop in numbers, although 1915 was another good year. Moors began to recover by about 1921, and by 1934 were again in good condition with high breeding densities. The 1939 war caused an even heavier and more general decline owing to two bad years in 1942 and 1944. Numbers are now, in 1951, again recovering, but there are reports of disease in some places; probably the recovery of the stock had been allowed to get ahead of burning as densities do not seem to have been high compared with pre-war years. Stocks should be good again by 1953–4 and crashes are likely to follow about 1954–5. They may be spread out over several years as in 1921–4.

Shooting is a form of predation, specialized in that it is exactly controllable and the game shot should be the surplus to the numbers which the ground will carry in winter and spring, the carrying capacity. It replaces to some extent natural factors such as predation, starvation, disease or forced migration, and implies some form of control of predators, which is good if not excessive. The main difference between shooting and natural predation is that the latter causes a steady drain the whole year round. Shooting replaces this with a heavy drain for a short time, keeping the ground over-stocked in summer and autumn when food supplies are good. With all the tetraonids, shooting falls heavily on the older birds in the year of a crash before it is realized the numbers have decreased. This may be an important factor in intensifying the drop. With ruffed grouse (*Bonasa umbellus* (L.)) King (1937) stresses the value of mature, 4–6-year-old birds in recovery.

Some American writers hold that predator control makes little difference to game stocks (Allee, Emerson, Park, Park & Schmidt 1949, pp. 375–6; Buss 1946; Leopold, Sperry, Feeney & Catenhausen 1943; Allen 1946; Einarsen 1945; Poole 1944; Schwartz 1945; Wilson & Vaughan 1944). In Great Britain, where the difference in numbers can be often seen on adjoining moors with different management standards, predator control makes a considerable difference to the numbers of game birds; but controlling predators allows buffer species to increase and they often compete with grouse for food. Foxes and crows do most damage, hawks being comparatively harmless.

(*d*) *Parasites*

The Grouse Committee believed that the immediate cause of death in crashes was strongylosis, that is infestation by the nematode worm *Trichostrongylus pergracilis* (Cobb). Practically all the 2000 grouse examined during 1906–09 (1912, p. 208) had a few worms, that is, the potential cause of death was always present. In bad years the worm is found in enormous numbers at the ends of heather shoots on which grouse mainly feed. Nothing can be done at this stage and it is still not known how this increase occurs. Outbreaks do not spread from one point, but occur in many places at the same, or about the same time.

Whether it is one of the primary causes of crashes or only a feature which sometimes accompanies and intensifies drops due to other causes, strongylosis occurs when numbers exceed the critical density, perhaps only temporarily. The density at which such overcrowding occurs varies from place to place, and in different years in the same place; bags may maintain about the same level for 2 or 3 years with a sudden crash in the next. One moor with a very high bag-acreage ratio had no disease between 1876 and 1944, yet the bag drops to 25 or 30% of peak level in or about crash years. As the policy here is to maintain a high breeding stock, the proportion of the August stock shot is lower when that stock is low than when it is high, and it is possible that the reduction in numbers may be partly due to emigration, perhaps in spring, to areas of low density but this is not proved. That immigration into understocked moors occurs is shown by the Grouse Committee's record already quoted (1912, p. 433). A bag of 3402 grouse in 1866; only four birds found on the moor in 1867; and bags of 530, 1621, and 3548 in 1870–2. It is impossible for these bags to have come from the progeny of only two pairs in 1867, therefore the birds came in from elsewhere. I have other cases almost as striking in my own figures. Conversely, it is probable that in some cases big drops on disease-free moors are partly due to emigration. That they are not entirely due to it is shown by Ireland and the Outer Hebrides, where drops occur in areas in which disease has never been recorded.

Ixodes ricinus L. the sheep tick sometimes causes heavy losses on certain moors, which may be difficult to let in consequence. See Darling (1947, p. 108) and Vesey-FitzGerald (1946, p. 27). The Grouse Committee (1912, p. 191) says it is rare on grouse, but this is not the case in some places to-day.

DISCUSSION

The data given show two aspects of what is essentially one fluctuation in British tetraonids. Grouse data cover the whole range of *Lagopus scoticus* and show that there is some synchrony throughout the range of both subspecies. This synchrony is not exact, but the majority of peaks both in large and small areas occur during a series of 'peak periods'; even when there is some divergence, peaks can be related to each other. That is, for instance, the 1905–7 group of peaks occur after the 1900–2 group and before the 1910–13 one. The exceptions, moors with peaks in the intervening years, are few, less than 12% occurring in 47% of the years between 1860 and 1943. Data for the other tetraonids show that in one area, central Scotland, the four species fluctuate at much the same times and in much the same way as grouse over their whole range. Such data as we have for blackgame outside this area show that the fluctuations in other districts tend to agree with those of the local grouse populations.

Before discussing the four species together, one or two features peculiar to grouse may be mentioned. Moors are divisible into two groups. In the first which lies mainly within the habitat of *L. s. scoticus*, disease is prevalent: in the other, mainly the habitat of *L. s. hibernicus*, disease has not been recorded. There are many moors in the *scoticus* area which are believed to have been free of disease when a crash occurred. One moor of a very high standard is said definitely to have been free between 1876 and 1944: the management is so good that it is inconceivable that an outbreak could be missed. Peak numbers are very high here, and a drop of 70% still leaves a density

at which other moors are vulnerable. No outbreak has been recorded from Bute, and Vesey-FitzGerald (1946) says that the island of Hoy is clear; but records from Mull and Skye show that islands are not *ipso facto* free. Since crashes of considerable magnitude, drops in the bag of over 80%, sometimes occur on moors in the disease-free area although not as often as within it, disease is not an essential even for a heavy crash and may not be part of the normal fluctuation mechanism, but only an accompaniment to a drop from other causes. The Grouse Committee's maps (Committee of Inquiry on Grouse Disease 1912) show disease outbreaks somewhere in every year between 1872 and 1909, although there were only two in 1884 and 1885, and only one in 1905 as against ninety-five in 1908, when the investigation was in full swing and reporting was good.

In parts of the grouse range there are no other tetraonids, and from their habitat on the open moor, snow is important for grouse. By itself snow is not serious; grouse are used to it. But when the surface is glazed and frozen, it presents a formidable obstacle to foraging. I have often walked round one day after snow seeing nothing, and on the next have put up considerable numbers of grouse from my tracks, where the crust was broken, and from nowhere else. I have also seen many grouse on deer tracks in snow, and Darling records this (1947, p. 94); see also Committee of Inquiry on Grouse Disease (1912, p. 25). Grouse congregate on the few open patches (often called black ground), and in years of abundance the density on these may be very high indeed, the ground being justifiably described as black with grouse. The vegetation becomes trampled and fouled, and especially if these conditions last for more than a few days, infested with *Trichostrongylus*. This seems the most probable cause of disease outbreaks.

But the degree of overcrowding, or indeed whether overcrowding occurs at all, depends on the density of the grouse, the size of the bare areas and the duration of unfavourable conditions as well as on other things such as the vegetation on the bare areas and the other species using them. In areas where disease has not been recorded density is low, and overcrowding in the above sense does not occur. The resources of the environment are, however, small, and numbers may be too great for them at other seasons.

In the Outer Hebrides and Ireland the whole habitat is wet and close to the limits of tolerance. In a good year, which probably means a dry year here, sites which are not of the best are used successfully, and when a bad season comes the broods in these poor sites do not survive. This is not proved, but if correct as I think, it would mean that in a wet season only the young birds from the best sites would get away while those from the bad ones would die. The result would be a reduction in numbers, but not as great a reduction as occurs when disease attacks the whole population, adults as well as young. This is in fact shown by the figures. The drops tend to be about 20–40% instead of 80% or more as is usual on single moors, although district figures may not show such a big drop owing to the smoothing effect of several moors differing slightly in their peak years. It is probable that the older birds occupy the best sites, the younger ones being pushed into marginal ground. So in bad seasons the least prolific class will be the successful one, which will increase the drop due to failure of certain nest sites.

At certain levels the stock is not likely to suffer heavy mortality from lack of resources. Numbers are so low that overcrowding does not occur under any but the most severe conditions which, if of frequent occurrence, would make the country unsuitable as a habitat and exterminate the species. After a crash the time taken for the stock to become liable to severe losses again depends mainly on the numbers shot, as predators have been controlled to such an extent that their toll is much reduced. The incidence of the best and worst conditions is usually widespread, but the results may vary from place to place, both with the local effects and the local state of abundance at the time. The Committee of Inquiry on Grouse Disease give an instance (1912, p. 282): in 1908 'A good deal of disease was reported. . . where the large stock had been left from 1907. On the other hand, from one district which had been swept by disease in 1907, the reports were excellent—well-filled nests, plenty of young birds, no disease.'

Management measures and standards have an important effect. Drainage improves a moor if it is wet, but may be bad on a dry moor, or on any moor in a dry year. If swamps provide a useful, perhaps essential, food in early spring, this supply may be seriously reduced. Yearly burning of small patches improves the juxtaposition and interspersion of cover types, nesting and feeding heather being near each other and so distributed that each potential nesting territory contains all such requirements as water, grit, ground with enough insects for chicks and cover for resting and roosting (which is generally the same as nesting cover). But all moorland is not equally suitable for grouse at all times, and artificial help such as draining and burning may increase nesting and rearing facilities to such an extent that after a good year when marginal sites are successful, there is liable to be overpopulation in autumn and winter. If the next season is not a good one, there is likely to be a poor rate of survival in the less favourable territories and a considerable drop in numbers without disease. This is thought to happen in the Outer Hebrides and Ireland, and sometimes to occur elsewhere. The general effects, then, are that: (1) a universally very good or bad year produces a crash which tends to be universal or nearly so, and brings the whole country into step periodically; (2) in a series of average years the occurrence of a crash on a given moor depends on local conditions, the stock left after the shooting season, and the exact local effect of such bad weather as there may be; (3) the combination of these with a fairly regular period for recovery produces crashes more or less at the same times, brought into line occasionally by one which is universal, and this is shown by the figures.

The area covered by this paper, the northern parts of the British Isles, is small compared with the ranges of some American animals. It is possible that a universally good year may never occur all over the bigger area, which would mean that fluctuations were never brought into line, and so would be irregular. See Griscom (1945, p. 18) for variation in peak dates of ruffed grouse in Massachusetts.

Local migration to neighbouring areas of low density may occur at any time, and it is probable that this is one cause of part at least of the drop on moors free of disease in the disease area. This is not to be confused with the annual movements between high and low ground which bring their own overcrowding problems. Caper and blackgame colonize young woods and probably also migrate on a small scale at other times. Ptarmigan when disturbed often fly to the next hill top.

The records show that peaks in the tetraonid populations are followed by drops of varying depth and suddenness, not always in the year following that of maximum abundance. Peaks are normally sharp and definite, but high densities may be maintained for 2 or more years. A peak or a series of years of high bags is usually followed by a drop of 50% or more, continuing for 2 or 3 years, but this is not always so. The drop may be smaller than this, and may rarely be for 1 year only with recovery in the next. Normally the drop is more sudden than the recovery, taking 2 or 3 years compared with 4 or 5, but management measures aimed at quick recovery often mask this by shooting lightly when numbers are low.

The periods vary from 3 to 10 years, but some degree of correlation is shown over the whole range. Most moors have peaks in about the same years, and for larger areas all peaks can be related to a particular peak period. At the same time, both the actual year of maximum numbers and that of the heavy drop may differ by as much as 4 years not only in whole districts, but on moors on the same estate. A peak may sometimes be missed altogether. Superimposed on this general agreement or loose periodicity, which holds for districts, areas of considerable size, is the fact that a few smaller units, moors, may have both peaks and crashes in any year whatsoever. A moor showing a peak out of step with the others on one occasion will generally coincide with them on others. Only 2 years show no maximal peaks in grouse, and only 1 shows no crashes.

There is no record of grouse disease or any similar disaster occurring in the other tetraonids. In spite of this their fluctuations show all the same features as those of grouse. 'Duplicate peaks' are more common, especially in ptarmigan and caper, and there is a tendency in all three species for an extra peak to be interpolated when the grouse interval is long, e.g. 1876. Peaks in caper and blackgame tend to be before rather than after those of grouse, and such an early peak is often associated with a duplicate peak.

Peaks and crashes may occur at different density levels, especially in small units. So overcrowding is a relative condition depending on the state of the factors of the environment at any particular time. While peaks usually occur in a given area at about the same level of abundance, under unfavourable conditions they may occur at a lower density and under exceptionally favourable ones (1912) at a higher one. For a good year all essential factors must be normal or favourable, while deterioration of a single factor may produce a bad one.

There is little data as to the underlying cause of these associated fluctuations. The varying interval seems to rule out any *regular* inherent rhythm. Strongylosis is perhaps the most prominent feature of drops in grouse, but in some areas it has never been recorded although drops occur (Bute, the Outer Hebrides, Ireland), and where it occurs some moors are sometimes free of it, although an increase in the over-all incidence accompanies periods of decline in numbers. It is therefore not an essential cause of crashes, although it often accompanies and intensifies them. It cannot be the cause of drops in the other species.

There seem to be two possible theories: the cause of fluctuations, correlated in four different species in one area, may be inherent in all of them, drops after overcrowding being due to some general decrease in vitality, a condition which is also

conducive to an increase in other adverse factors such as strongylosis or bad nesting seasons; or good or normal seasons allow a regular increase, the cause of drops being multiple, any one of them coming into action according to such things as the degree of overcrowding and the exact local incidence of various unfavourable factors, mostly climatic in ultimate origin except for undershooting. On the first theory, numbers drop from increased deaths and decreased reproduction and survival, and the unfit birds become liable to various calamities because they are not quite fit and healthy. It seems unlikely that such a general lowering of vitality or viability will affect four different species in the same way every few years at about the same time. Although related the species show considerable differences in habitats and tolerations. The moor is a more exposed and severe environment than woods or scrub, and mountain tops over 3000 ft., largely bare rock and scree, are harder than either woods or moor; although the micro-climate amongst vegetation is different from that a foot or two above it, rainfall, mist and cloud (relative humidity), wind, sunshine and temperatures are all of a different order, and the same applies to different districts such as the Isles and the west coast, and the east and centre. On the second theory, the action of any one adverse factor will decrease overcrowding and so inhibit that of others occurring afterwards. An outbreak of disease early in the year reduces numbers so that other adverse factors do not operate later. With no disease, competition for nest sites is intense and marginal nest sites are used which are lethal under adverse conditions such as excessive rain. If the weather is good and the hatching rate high, the chicks are subject to competition for food and to outbreaks of coccidiosis. This would be parallel with the results of human overcrowding where population decreases are caused by many different agencies, plague, cholera, smallpox, famine, war and emigration. The cause varies but the result is the same.

The four species occupy different habitat niches, in which the direct effect of external factors will differ. For instance, snow blankets a moor but is broken up in woods and leaves tree buds and needles exposed. It freezes and forms a crust at low levels, but tends to remain comparatively soft on high ground as it does not thaw. The direct effect of climate varies both locally and interspecifically.

The only common factor I can see is food, which is vegetable in all four species. If year to year climatic variations affect the quality or quantity of vegetation, this would affect all four species in the same way, although perhaps not to the same degree. The berry crop, blaeberries, crowberries, etc., varies widely from year to year, as do the seed crops of trees. The heather flourish and seed crop varies; a wet autumn almost certainly reduces pollination and seed—it certainly reduces the honey crop. The appearance of a hill one knows well varies from year to year, probably with the amount and kind of grass seed. So some foods taken by all four species definitely vary in quantity, and others probably do so, just as farm crops vary. Any scarcity is most severely felt when numbers are high and may be due to all or any of a number of adverse climatic factors—late frost, wet weather, low temperatures, drought. The position may be pejorated by competition with other animals, rabbits, sheep or insects. With no definite data, it is unprofitable to speculate further; but it is relevant that there are indications in dendrochronology that years of good tree-growth usually occur in tetraonid peak periods, while prices of hill sheep in Scotland have reached

peaks in the last hundred years in those same periods (Hustich & Jones 1947; Schove 1950; but see also Dobbs 1951; Lemmon 1949). Tree-growth variations are largely if not entirely dependent on climate, while high hill-sheep prices in one small unit of the world market presumably reflect the quality of the food available on the hill, and its effect on weight and wool.

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SUMMARY

1. Bags of British tetraonids are given from game books. Red grouse are from some eighty moors spread over the range of both subspecies, and the oldest records go back to 1834. Peaks are shown and some records of disease outbreaks back to 1797 are noted. Bags of the other tetraonids from a number of estates in central Scotland from 1866 to 1949 are also given.

2. Some notes on the ecology of all four species are given as far as they may affect fluctuations.

3. *Lagopus scoticus* fluctuates throughout its range, the period being irregular, between 3 and 10 years but mostly 5 or 6. Peaks may sometimes be missed in some units, but there is a general synchrony which is not however exact. Peak years may differ even on adjoining moors. It is suggested that this synchrony is brought about because, while crashes on each moor are due to the interaction between the birds and their immediate environment, there is occasionally a very good or very bad year which brings big areas into line.

4. The critical density may differ in the same area in different periods and varies widely from place to place. Where density is high, strongylosis is often but not always associated with crashes. Cycles with much the same rhythm and dates occur in areas where it is unknown, when bad nesting seasons are thought to be the limiting factor. Some of the worst crashes occur when they are associated with strongylosis.

5. A possible explanation is that once the critical density is exceeded or resources are reduced below requirements (perhaps only temporarily) the particular agency which reduces numbers may vary.

6. The other three tetraonids show rises and falls more or less synchronously with grouse. The exceptions and statistical correlation are discussed.

7. Duplicate peaks sometimes occur at intervals of 2 years only. Species other than grouse sometimes have interpolated peaks in long intervals.

8. It is suggested that the only common factor likely to cause these events is food supplies, which are themselves affected by weather.

9. Peak periods of 2 or 3 years are suggested, during which most peaks occur. Exceptions and causes are discussed.

10. Blackgame bags from south Scotland from 1850 to 1949 are given and agree in general with data from central Scotland.

11. An increase in warmth and wetness in the northern climate may be the ultimate cause of the long-term variations.

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APPENDIX

ANNUAL BAG FIGURES

Total annual bags of samples, by districts, peak years (maximal bags) in heavy type. All figures are ×100, and superscript figures give the number of moors in the sample whenever there is a change; letters show the peaks in individual moors. Vertical lines on the left of the date column indicate peak periods for all species; lines on the right show the peak periods for grouse only (see p. 133).

	Red grouse												Scotland, central			
Year	Scotland, south	Atholl	Scotland, central	Scotland, north-east	Scotland, north-west	Scotland, west	England, east and central	England, west	Wales	Total	Hebrides	Ireland	No. of moor peaks	Ptarmigan	Capercailzie	Black-game	Scotland, south Black game
1834	2[3]	.	.	.	.	.	.	.	.	2[3]	.	.	.	.	.	.	.
1835	5	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.
1836	5	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.
1837	11e	.	.	.	.	.	.	.	.	11	.	.	1	.	.	.	.
1838	9d	.	.	.	.	.	.	.	.	9	.	.	1	.	.	.	.
1839	9e	.	.	.	.	.	.	.	.	9	.	.	1	.	.	.	.
1840	10cd	.	.	.	.	.	.	.	.	10	.	.	2	.	.	.	.
1841	8	.	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.
1842	9	.	.	.	.	.	.	.	.	9	.	.	.	.	.	.	.
1843	12	.	.	.	.	.	.	.	.	12	.	.	.	.	.	.	.
1844	19c	.	.	.	.	.	.	.	.	19	.	.	1	.	.	.	.
1845	17d	.	.	.	.	.	.	.	.	17	.	.	1	.	.	.	.
1846	17e	.	.	.	.	.	.	.	.	17	.	.	1	.	.	.	.
1847	12	.	.	.	.	.	.	.	.	12	.	.	.	.	.	.	.
1848	15	.	.	.	.	.	4[1]	.	.	19[4]	.	.	.	.	.	.	.
1849	20	.	.	22[1]	.	.	4	.	.	46[5]	.	.	.	.	.	.	.
1850	27	.	.	24	.	.	5	.	.	56	.	.	.	.	.	.	19[8]
1851	32c	.	.	26	.	.	5	.	.	63	.	.	1	.	.	.	15
1852	29[4]	.	.	26	.	.	9	.	.	64[6]	.	.	.	.	.	.	14
1853	45bde	.	.	45	.	.	12a	.	.	102	.	.	4	.	.	.	25
1854	32c	.	.	53a	.	.	7	.	2[1]	94[7]	.	.	2	.	.	.	15
1855	26	.	.	22	.	.	6	.	2	56	.	1·6[1]	.	.	.	.	24
1856	26	.	.	7	.	.	7	.	2	42	.	1·5	.	.	.	.	24
1857	23	.	.	21	.	.	8	.	4a	56	.	2·2v	2	.	.	.	28
1858	43	.	.	29	.	.	6	.	2	80[9]	.	1·6	.	.	.	.	21
1859	51[6]	.	11[2]	44a	.	.	9	.	4a	119[11]	.	1·4	2	.	.	.	26
1860	58ad	.	14	39	.	.	10a	.	2	123	.	1·0	3	.	.	.	24
1861	59bcei	.	21do	0	.	.	6	.	4	90	.	1·1	6	.	.	.	36
1862	24	.	10	7	.	.	2	.	4a	47	.	1·3	1	.	.	.	8
1863	28	.	9	19	.	.	2	.	3	61	.	1·4	.	.	.	.	13
1864	65	.	20	26	.	.	10	.	4	125	.	1·4	.	.	.	.	27
1865	118	.	22	47	.	.	17	.	5	209	.	2·2v	1	.	.	.	32
1866	203abcdei	157[16]iklmnoq	34do	57a	.	.	34a	.	9a	494[27]	.	1·3	18	1·6[8]	1·4[8]	4[17]	25
1867	5	149bdefghjp	12	0	.	.	0	.	6	172	.	1·3	8	1·3	0·6	3	3
1868	11	97	14	0	.	.	0	.	2	124	.	1·2	.	0·8	0·3	4	1
1869	34	95	13[3]	16	.	.	0	.	3	161	.	1·5	.	0·3	0·4	5	29
1870	81	150b	25	22	.	.	8[2]	.	2	288[28]	.	1·5	1	0·6	0·6	7	31
1871	153abcdi	195degjmoq	53h	60	.	.	53	.	6	520	.	2·0	13	0·5	1·3	9	29
1872	144e	183fhiklnp	25de	106a	.	.	83ab	.	9a	550	.	2·5	14	0·9	0·9	4	21

APPENDIX (*cont.*)

Year	Red grouse: Scotland, south	Atholl	Scotland, central	Scotland, north-east	Scotland, north-west	Scotland, west	England, east and central	England, west	Wales	Total	Hebrides	Ireland	No. of moor peaks	Scotland, central: Ptarmigan	Scotland, central: Capercailzie	Scotland, central: Blackgame	Scotland, south Blackgame
1873	8	44	11	5	.	.	1	.	1	70	.	2·6	.	0·2	0·6	3	3
1874	20	25	10	6	.	.	1	.	2	64	.	6[2]	.	0·2	**1·0**	6	17
1875	60	30	11	10	.	.	5	.	3	119	.	7v	1	0	1·0	5	**21**
1876	**114**adi	82g	31dh	19	.	.	12a	.	**5**a	273	.	**9**[3]aw	10	0·1	0·9	**10**	18
1877	109be	128iopq	29e	**23**a	.	.	12	.	3	**304**	.	4	8	0·3	0·7	5	13
1878	64	134	29	12	.	.	**52**b	.	1	292	9[1]	7	1	0·6	0·6	8	18
1879	73	174d	32	19	.	4	22	.	2	326[29]	10	6	1	0·7	0·6	5	10
1880	69	181efo	34e	21	.	6	27a	.	1	339	11	**11**vw	7	**1·5**	1·3	**8**	**20**
1881	89b	**192**bhijkm	31	34[2]	.	**6**a	33	.	3	388[30]	11	1[1]	9	1·2	**2·0**	6	14
1882	**112**adi	149lnpq	**44**[4]d	**48**a	.	5	41	.	**4**a	**403**[32]	**12**	0	11	0·8	1·3	4	15
1883	64	89	39	35	.	3	43	.	3	276[34]	0	1	.	0·6	**1·9**	4	14
1884	81	105g	51	38	.	3	46	.	3	327[37]	0	1	1	1·1	1·3	4	9
1885	146	119	47e	27	.	5	**54**b	.	14[2]	412	0	2	2	1·0	0·9	5	12
1886	**229**abei	137	58[5]	38b	.	4	41	.	13	520[34]	3	2	5	**2·2**	0·8	3	15
1887	144	188d	70	**47**a	**29**[3]bc	4	46	.	16	544[37]	2	4[2]	4	1·7	**2·4**[10]	**5**[19]	**17**
1888	201c	**221**cefhk lmnoq	**87**dhk	29	19	**9**a	41	.	16a	**623**	6	**6**af	18	1·1	1·6	4	15
1889	123d	175bij	40f	29	23a	1	66	.	**16**b	473	8	5	7	1·2	**2·5**	3	13
1890	200ac	169p	57	29	**24**b	1	**83**ab	.	15	578	13	5[3]	6	1·4	1·8	2	13
1891	119	123g	48	44	19	0	29	.	12	394	**16**	4	2	**1·9**	1·6	3	**17**
1892	150	70	39[6]	51	6	3	29	.	12	360[38]	9	4f	1	0·4[9]	1·3	1[20]	12
1893	224	92	50	**52**b	9	1	82b	.	3	513	7	4	2	0·7	1·7	4	14
1894	238b	111bj	49k	50a	7	6	**83**a	.	21	565[39]	4	10[5]ay	8	1·0	1·1	3	20
1895	261	130oq	**60**bh	22[3]	13b	4	37	.	27	554[40]	4	11	5	0·2	1·3	3	**21**
1896	**340**acdei	145n	41de	33	**16**ac	9	66b	.	**30**ab	**680**	4	13v	14	0·8	**2·7**	**4**	20
1897	106	**171**cdegm	32	32c	10	**20**ab	65a	.	17	453[41]	4	**14**fx	11	**1·2**	1·1	3	10
1898	156	158f	38	48	7	1	59	.	21[4]	488[42]	5	12	1	0·7	1·1	5	15
1899	182	170	49[7]	72	17	9	52	.	39b	590[43]	6	**14**v	2	1·1	1·3	5	17
1900	199ai	227bcdko	49	**105**ab	**18**bc	7	28	61[2]	59	753[45]	**6**	12axy	15	**1·5**	**1·7**	6	16
1901	**245**be	**247**fhijlmnp	**162**[11]bhijk lmn	94c	17a	17a	**61**b	**91**a	**91**abe	**1025**[49]	6	10f	27	1·3[11]	1·5[14]	**7**	26
1902	242cd	162eq	84f	54	11	20	52a	84b	60c	768	6	9	8	0·5	1·0	5	**30**
1903	135[6]	109	101h	36	12	18	38	61	41a	551[48]	3	8	2	0·8	2·3[15]	3	20
1904	187	116	63[12]	33	12	**30**b	**52**b	64	66	622[49]	6	9	2	**2·0**	1·7	5	22
1905	**259**ce	173c	92	29[2]	18a	25	48[1]	74a	**82**be	800[47]	**7**	**11**vx	10	1·5	**3·0**	**9**	28
1906	226b	**220**eghijklm nopq	**123**bdefgh jklmn	35	**23**b	**29**ab	21	**82**	62ac	**821**	6	11ay	31	**2·0**	2·8	8	**31**
1907	230di	148d	100[13]i	**43**bc	19	21	31	78b	57	726[48]	6	8	7	0·5	2·1	4	24
1908	190	139f	75	20	18	16	**54**b	38	51	600	5	10	2	**1·9**	**3·3**	6	30

1909	186	108	43	25	19a	24	51	49	21	526	4	7^{6}f	2	0·9	1·9	5	30
1910	265	106	81	**56**bc	**20**bc	36	34	111	76	784	**5**	9	5	1·5	2·6	**10**	**41**
1911	467c	145o	140bgm	24	14	43b	46b	**160**ab	88	1128	5	**12**	8	1·0	**2·7**	7	34
1912	**579**de	**281**abcgijkl mnpq	**162**adehij kln	30	11	**54**a	135^{2}	84	**103**e	$\mathbf{1439}^{49}$	4	14x	25	0·8	2·6	6	25
1913	139fg	174def	43f	16	5	53b	**188**bc	64	93abc	776	3	**17**atvy	16	**1·2**	2·5	5	21
1914	138	131	58j	24	5	30	103	45	52	587	3	10	1	$0{\cdot}4^{12}$	1·6	4	26
1915	**282**cd	$\mathbf{172}^{18}$abdefh mnopq	**81**aehikmn	**51**bc	**8**b	26b	**180**c	77	52	$\mathbf{929}^{51}$	**4**	7^{5}	26	0·3	1·0	**7**	**43**
1916	280eg	99g	41	3	6c	26	133	86	48b	722	2	7	5	0·4	1·0	3	31
1917	122f	60^{19}j	32g	3	4	13	84	**102**ab	30	450^{52}	2	7	5	0·4	1·2	4	25
1918	66	56s	31	4	2	5	68b	81	19	332	2	8^{6}b	3	0·5	**1·5**	4	22
1919	86	54	43	13	0	12a	38	46	24	316	**1**	**9**at	3	0·7	1·0	4	17
1920	136d	105oq	81	34	2	10	44	37	15	463	1	9	3	1·8	0·9	6	**20**
1921	**148**cefg	$\mathbf{170}^{20}$abcimr	**128**jkn	**58**bc	5	18	82c	**66**ab	27a	$\mathbf{703}^{53}$	1	7	19	1·6	2·5	**9**	17
1922	61	**210**defhjks	$\mathbf{94}^{14}$bm	37	**9**b	15	57	37	31	551^{54}	**2**	**9**v	12	**2·9**	**3·2**	7	8
1923	83d	170bilt	133af il	10	6c	24b	**94**bc	28	34e	582	2	7	14	2·4	2·5	5	11
1924	82	139gmnopqr	**135**cdeghjkn	20	6	**24**a	40	22	**39**c	507	2	7^{7}x	18	2·5	1·8	4	10
1925	44	51a	53^{18}	21	7	9	38	11	34	268^{53}	2	7^{8}	1	0·9	1·1	4	10
1926	128^{6}g	78	91	**32**bc	10a	16	130	34	43	561^{54}	2	10	4	0·3	**1·4**	**5**	**14**
1927	**207**cefh	98^{19}bopqu	**104**bcejmn	10	12c	21	**186**bc	**84**ab	42	$\mathbf{764}^{53}$	2	14^{9}a	21	**0·7**	0·8	4	11
1928	173d	107de	80g	9	10b	**30**ab	28	7	43	487	1	17^{10}v	8	0·3	0·8	4	7
1929	105	$\mathbf{123}^{18}$cf ijlr	130i	14	11	16	28	11	47b	485^{52}	0	14^{8}bcd	11	0·7	0·8	5	6
1930	**187**cd	115bghmnqtu	152behm	39	13	17	**100**c	30a	**59**ace	**711**	1	19tx	20	0·6	0·8	**7**	**10**
1931	160fgh	85a	168c	**45**bc	14	20	76b	**50**b	22	640	1	19fey	12	**1·7**	**1·1**	5	8
1932	103	98f	172dg	9	15	**26**b	28	13	28	492	2	19	4	1·6	0·6	7	9
1933	211e	**156**abcdeght	**257**aijklmn	18	25	25a	119	38	47	895	2	**24**a	18	**3·5**	**1·2**	**8**	13
1934	**257**cdfg	139jlmnrsu	211bceh	**40**b	33abc	12	**194**bc	**85**ab	57e	**1028**	**3**	22bt	27	2·2	**1·5**	7	**18**
1935	117h	86^{15}q	165	39c	26	5	80	49	**60**abc	627^{49}	2	19cdxy	10	1·0	0·6	4	10
1936	84	68^{14}	151g	26	15	5	83	51	28	$\mathbf{511}^{48}$	2	14^{9}	1	2·4	0·6	3	9
1937	128	84degu	107d	9	8	7	86	36c	24	489	**3**	11	7	2·2	**1·2**	2	8
1938	**150**dfgh	**97**abcfhi lmst	**172**chijkln	12	**10**bc	**11**ab	46	**40**a	22c	**560**	2	11c	28	**2·4**	1·1	2	4
1939	43	49	50b	**16**c	5	7	6	0	17e	193	**3**	13z	5	1·8	0·3	1	2
1940	103	44eu	35	10	1	10	14	25	12	253	1	$\mathbf{15}^{8}$ay	4	1·0	0·5	1	2
1941	**156**cdefgh	36abf	**45**deijn	**11**b	3	8	27	76	11^{3}b	$\mathbf{373}^{47}$	0	11btx	19	0·8	**0·7**	**2**	**4**
1942	89	22	36	2	3	3	**33**	**91**a	8c	287	0	7	2	0·9	0·6	1	2
1943	24	20^{13}gmt	**56**abghk	2	2	1	28b	73b	5	$\mathbf{211}^{46}$	0	5	10	0·4	0·1	1	2
1944	17	6^{10}	10^{8}	1	1	1	3	1	6	46^{38}	0	4	0	0·4	0·4	0	1
1945	12	6^{7}	2^{4}	1	0	0	1	9	3	34^{31}	0	5a	1	0·2	0·1	0	1
1946	.	.	.	.	.	.	8	15	2	.	0	6txz	.	0·2	0·3	0	1
1947	.	.	.	.	.	.	.	23	2	.	0	4	.	0·2	0·2	0	1
1948	.	.	.	.	.	.	.	91a	2	.	0	6	.	.	.	Rising	1
1949	.	.	.	.	.	.	.	86b	3	.	2	9	.	.	.	.	1
1950	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Approx. max. acreage (thousands)	160	100	90	20	20	30	30	15	23	488	30	97	.	.	.	.	.

THE STATISTICAL ANALYSIS OF GAME-BIRD RECORDS

By P. A. P. MORAN
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In the preceding paper, Mr J. M. D. Mackenzie has given some remarkable data for the annual bags of grouse, ptarmigan, capercailzie and blackgame on a number of Scottish estates from 1866 onwards. In the present paper we subject this data to statistical analysis. The main question we wish to answer is whether these series provide evidence that the populations are fluctuating independently of each other or not, but in the course of examining this we shall also consider what evidence there is for 'cyclic' or 'oscillatory' tendencies. The natural statistical approach to the first question is to calculate the ordinary correlation coefficients† between the series. These are given in Table 1 (the asterisks will be explained later).

Table 1. *Correlations between game-bird series*

	Ptarmigan	Caper	Blackgame
Grouse	0·504 (**)	0·504 (**)	0·347 (*)
Ptarmigan	—	0·417 (*)	0·052
Caper	—	—	0·189

These correlation coefficients, which are all positive, were calculated from the bags for the years 1886–1938, inclusive. The bags for 1939 onwards were omitted in order to avoid the effects of the second World War. The results during and immediately after the first World War were not omitted because if they had been, the later calculations would have been much more awkward. The series do not, however, seem to have been very much affected at that time. The same set of years, 1866–1938, were also used in all the subsequent calculations.

We now ask whether these correlation coefficients are statistically significant, i.e. whether they are larger than might have reasonably come about by chance. In ordinary circumstances this may be determined by applying a standard significance test. The use of such a test, however, is only valid when the observations, in at least one of the series, are independent of each other. If this is not true and the value at any one year of each of the series is dependent in some way on the values of previous years the mathematical assumptions underlying the test of significance of the correlation coefficient are no longer true, and misleading results will be obtained. There has been a wide misunderstanding of this point amongst biologists and economists (see Moran, 1949). In the present case it seems likely that there should be some kind of serial dependence since the birds in any one area in any one year are the descendants of the birds in that area in previous years. We therefore test the series for serial dependence by calculating and testing the serial correlation coefficients.

† The comparison of 'peaks', and other such methods, are not only less efficient but also do not allow tests of significance to be made.

The definition of the serial correlation coefficient r_s of lag s, which we use, is

$$r_s = \frac{n}{n-s} \frac{\sum_{i=1}^{n-s} x_i x_{i+s} - (n-s)^{-1}\left(\sum_{i=1}^{n-s} x_i\right)\left(\sum_{i=s+1}^{n} x_i\right)}{\sum_{i=1}^{n} x_i^2 - n^{-1}\left(\sum_{i=1}^{n} x_i\right)^2}, \tag{1}$$

where n is the number of terms. The conventional factor $n(n-s)^{-1}$ is introduced because the numerator is based on the sum of $(n-s)$ products and the denominator on the sum of n squares. As we are also correcting for the sample mean we might just as well have used $(n-1)(n-s-1)$ instead, but the difference is not important. A number of other definitions are sometimes used but give very similar results. (1) was chosen purely for convenience of calculation. Although it is only r_1 that would be normally used to test serial independence in a case of this kind we have also calculated r_s for $s=2, \ldots, 12$ as these throw light on the structure of any 'random process' which we may have to assume as a model for the generation of the series. Table 2 gives the values of r_s, $s=1, \ldots, 12$ for each of the four series.

Table 2. *Values of the serial correlation coefficient* r_s

s	Grouse	Ptarmigan	Caper	Blackgame
1	0·643	0·483	0·592	0·427
2	0·215	0·275	0·451	0·227
3	−0·003	0·029	0·337	−0·004
4	−0·062	−0·023	0·223	0·032
5	−0·001	−0·107	0·220	0·108
6	0·040	−0·283	0·129	0·024
7	0·026	−0·211	0·136	0·032
8	0·057	−0·301	0·074	−0·102
9	0·235	−0·106	0·134	0·018
10	0·299	−0·018	0·089	−0·002
11	0·222	−0·030	−0·004	−0·024
12	−0·020	−0·059	−0·081	−0·157

We must now test the significance of r_1 in each of these four cases. The exact distribution of r_1, as given by (1), under the assumption that the series are serially independent, is not known but it can be shown that, under such assumptions, the expected value is $-(n-1)^{-1}+$terms of order n^{-2}, and the variance of r_1 is $(n-2)^2(n-3)^{-3}+$terms of order n^{-2}. Using these results we see that r_1 for all four of the series is quite significantly different from its expected value. It follows that the ordinary test of significance for a correlation coefficient between any two of these series cannot be applied since the series are serially correlated.

However, it is possible to use an approximate test due to Bartlett (1935) (see also Moran 1949). If we have two independent time-series generated by stationary (e.g. without trend) random processes whose true serial correlation coefficients are ρ_s and $\bar{\rho}_s$ respectively, then in large samples (of length n, say) the sample serial correlation coefficient between the two series has a standard error whose square is approximately

$$(n-1)^{-1}\left\{1+2\sum_{1}^{\infty}\rho_s\bar{\rho}_s\right\}. \tag{2}$$

If we can estimate this expression, we can use it to provide a test of significance, either by comparing the observed correlation coefficient with its standard error, or

better still, by assuming that it is distributed as an ordinary correlation coefficient with n^* degrees of freedom where

$$n^* = (n-1)\left\{1 + 2\sum_{1}^{\infty} \rho_s \bar{\rho}_s\right\}^{-1}. \tag{3}$$

However, we cannot use this formula simply by substituting the observed values of r_s for ρ_s and $\bar{\rho}_s$, as it can be shown that this tends to lead to an incorrect answer. What we have to do is to construct a theoretical model for each of the series, fit it, show that it is an adequate representation and then use it to calculate ρ_s for all s.

The simplest such model, and one which seems very plausible for each of the above four series, is got by supposing the data to be generated by a relationship of the form

$$x_t = \rho x_{t-1} + \epsilon_t, \tag{4}$$

where $|\rho| < 1$ and the ϵ_t are a completely random sequence with zero means and the same standard deviation. It can be shown for such a model that the theoretical serial correlation is then given by

$$\rho_s = \rho^s \quad (s = 1, 2, \ldots). \tag{5}$$

The model is fitted by using r_1 as an estimate for ρ_1 and thus ρ_s is estimated as r_1^s. If in the other series we have $\bar{\rho}_s = \bar{\rho}^s$, then (3) becomes

$$n^* = (n-1)\left\{\frac{1-\rho_s\bar{\rho}_s}{1+\rho_s\bar{\rho}_s}\right\}. \tag{6}$$

More complicated schemes than (4) can also be fitted, but our first task is to see whether (4) provides an adequate model for the four series.

We may apply two types of test to the serial correlations given in Table 2. These serial correlations appear to be well fitted by a theoretical scheme like (5) since the observed serial correlations, in the ptarmigan, caper and blackgame series at least, tend to fall off to zero in the right way. For ptarmigan $r_8 = -0{\cdot}301$, and for grouse $r_{10} = 0{\cdot}299$ but these do not appear to be significantly different from estimated theoretical values (for tests of this type see Bartlett 1946). It is also possible (Quenouille 1949) to test the scheme (4) by fitting a scheme of type

$$x_t = ax_{t-1} + bx_{t-2} + \epsilon_t, \tag{7}$$

and testing whether the estimated value of b is significantly different from zero. This is equivalent to testing the partial serial correlation coefficient

$$\frac{r_2 - r_1^2}{1 - r_1^2}.$$

For ptarmigan, caper and blackgame this quantity is not significantly different from zero but for grouse it is significant. This appears to indicate that a model of type (7) would result in a better fit for the grouse series and that the latter, unlike the others, has a slight, but heavily damped oscillatory tendency. If this is real, its biological explanation is not clear. However, the important thing to ensure here is that we do not underestimate the quantity in brackets in equation (3). We can be quite safe in taking the possibly incorrect model of equations (4) and (5). This is made more evident if we consider what the values of ρ_s would be: (*a*) assuming a model of the type of equation (7) and estimating a and b by least squares; (*b*) assuming a model of

the type of equation (4) and assuming $\rho_1 = 0{\cdot}6425$; (*c*) as for (*b*) with $\rho_1 = 0{\cdot}7$. The resulting estimated values of ρ_s are shown in Table 3.

Table 3. *Estimated values of ρ_s for grouse*

s	Model (*a*)	Model (*b*)	Model (*c*)
1	0·643	0·643	0·700
2	0·215	0·413	0·490
3	−0·031	0·265	0·343
4	−0·099	0·170	0·240
5	−0·075	0·109	0·168
6	−0·031	0·070	0·118
7	−0·001	0·045	0·082
8	0·009	0·029	0·058
9	0·008	0·019	0·040
10	0·004	0·012	0·028
11	0·001	0·008	0·020
12	−0·001	0·005	0·014

We have now to consider how we should estimate the values of ρ in equation (6). It is known that (if the model of equation (4) is the correct one) r_1 is an asymptotically best estimator for ρ_1. However, Orcutt (1948) has shown that, for short series at least, it is a fairly heavily biased estimator and tends to underestimate the true value. Instead, therefore, of using the values 0·643, 0·483, 0·592 and 0·427, we shall take 0·7, 0·55, 0·65 and 0·5 for the grouse, ptarmigan, caper and blackgame series respectively. The effect of this is to put us well on the safe side in testing ρ. Table 4 shows the resulting values of n^*.

Table 4. *Values of n^**

	Ptarmigan	Caper	Blackgame
Grouse	32	26·9	34·6
Ptarmigan	—	34·1	40·9
Caper	—	—	36·7

Applying these values of 'effective degrees of freedom' to the correlations in Table 1 we see that those marked '**' are certainly significant at the 1% level and those marked '*' at the 5% level. The correlation between ptarmigan and caper is in fact very near the 1% level. These are, of course, not exact tests since we are guessing the ρ's, but we have allowed such a wide margin for safety that the conclusions can scarcely be doubted. Even if we had taken values of ρ equal to 0·8, 0·7, 0·7 and 0·6 respectively, the three correlations between grouse, ptarmigan and caper would still be found to be significant. The overall picture is, therefore, that these three series are definitely related, and that blackgame, although there is fairly strong evidence that it is related to grouse, is apparently little related to ptarmigan and caper.

One other point deserves attention. The actual bags can only be regarded as estimates of game population in the area shot over. It follows that (4) cannot be regarded as a completely satisfactory model. A better model would be obtained by writing

$$x_t = y_t + z_t, \tag{8}$$

where y_t is a series generated by a model of type (4) and z_t is a series of completely random terms representing an 'error of measurement'. The fitting of such a model is rather more complicated and seems very unlikely to give different conclusions.

The statistical methods used in the present paper are both approximate and tricky. It is not suggested that they can be widely or easily used, and they give a definite result in the present case only because the evidence in the series is so definite.

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A HAND-OPERATED QUANTITATIVE GRAB FOR SAMPLING RIVER BEDS

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(With Plate 3)

The accurate quantitative sampling of the bottom-fauna of rivers too deep to wade has long been a problem. The methods available hitherto have depended upon some type of dredge acting at the end of ropes. This principle involves several disadvantages:

(*a*) The apparatus tends to veer from the vertical when being lowered to the bottom in a strong current, so that the jaws do not meet the substratum squarely and the position of sampling is not known accurately.

(*b*) The operator is unable to bring his own power to bear on the jaw-closing mechanism without tending to pull the apparatus away from the substratum. In those dredges in which the closing action of the jaws depends upon their weight, the combined weight of the apparatus and its sample may well require the use of hoisting gear, and those in which the jaws are spring-operated are restricted to the sampling of soft sediments.

(*c*) It is difficult to sample on a sloping surface.

A grab is described here which overcomes these disadvantages; it consists of a long steel tubular handle, at the end of which is a box fitted with toothed jaws operated, from the end of the handle, by means of a steel operating rod moving within it.

The body and open jaws form a box with a toothed edge, (Pl. 3*B*) which, when lowered on to the substratum and pushed in to the extent of the teeth, forms a complete trap, the entire contents of which are lifted into the body of the grab as the jaws are closed, the closing action being effected by a downward pressure on the operating rod.

Thus, at each operation comparable samples are taken, the samples are quantitative and the position from which each sample comes is known with accuracy. The operator's action of closing the jaws tends to press the grab into the substratum and the apparatus is under the direct control of the operator in fast currents and on sloping surfaces.

In detail, the box, which is domed, is 9 in. long, 6 in. wide and $4\frac{1}{2}$ in. deep to the roof of the dome. Each end of the box is formed by a $\frac{1}{12}$ in. steel plate bearing seven teeth and is wide enough at the level of the jaws to cover the ends of the latter when fully open (Pl. 3 *B*, *C*). The end-plates bear a flange 1 in. wide which is welded on $\frac{5}{8}$ in. below the hinge-line of the jaws to prevent the grab from sinking too far into soft deposits. To each end-plate is welded a stirrup $1\frac{1}{2}$ in. wide, which bears at its centre a socket, threaded internally to take a steel tubular handle $\frac{5}{8}$ in. in diameter. The stirrup is strengthened by a web of $\frac{1}{16}$ in. steel welded to its centre-line and to the dome of the box (Pl. 3 *A*, *E*).

The jaws, which are of $\frac{1}{8}$ in. steel, are hinged along the whole length of the box and bear teeth which are $1\frac{1}{2}$ in. long and $1\frac{1}{4}$ in. apart. The teeth are hand-filed to interlock accurately when closed. Two small lugs on the inside of each end-plate prevent over-closing of the jaws, and the clearance between the jaws and the end-plates is very fine.

A gauze-covered slit 2 in. long and $\frac{3}{16}$ in. wide in the dome of the box allows air to escape from the grab when being lowered (Pl. 3 *C*).

The operating mechanism consists of a pair of linkage bars of $\frac{1}{4}$ in. steel, each bar being linked at its lower end to a fitting riveted on to the jaw and, at its upper end, to the flattened end of the operating rod which runs up inside the tubular handle (Pl. 3 *A*, *D*). The linkage spindles are secured with washers and split pins. The jaws are closed, from the fully open position, by a downward movement of the operating rod of four inches.

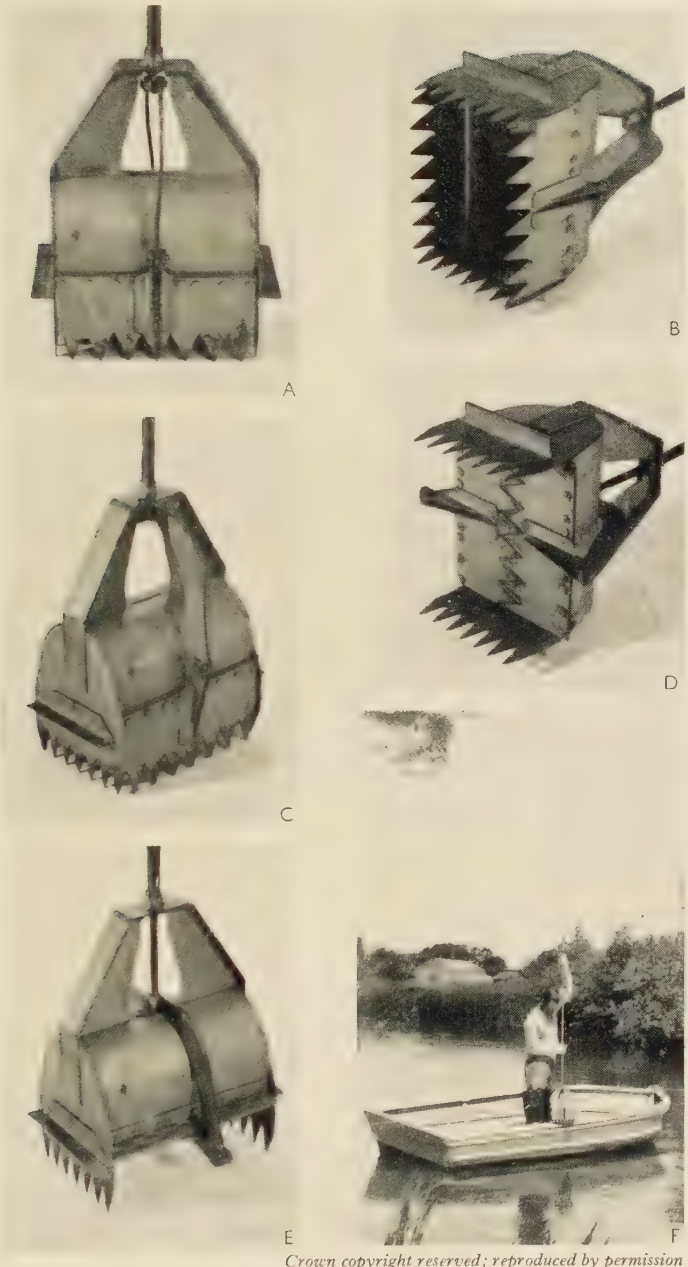
The tubular handle, which is 4 ft. 4 in. long (including the threaded inch which screws into the stirrup socket) and the operating rod, which is 5 ft. long, are both provided with a T grip, that on the latter, only, being removable and secured by a washer and wing-nut. When the grab is to be used in depths over 5 ft. the tubular handle is replaced by an extension tube 4 ft. 6 in. long and bearing a socket similar to that on the stirrup and into which the tubular handle is then screwed. The operating rod is lengthened by screwing on an extension rod, to the end of which the T grip is transferred. It was found possible to sample in 11 ft. of water, and the conversion to deep sampling can be carried out in less than 2 min.

The comparatively light weight (18 lb. with the short handle, 23 lb. with the extension) makes it very suitable for use from a rowing boat or other light craft (Pl. 3 *F*) the successive samples being flushed out into buckets with a hand pump for sieving.

This grab has been given thorough field trials during three long periods of river bed sampling in 1950 and 1951 and has been tested on types of substrata varying from very fine mud to large, compacted gravel. Its efficiency depends upon the degree to which the teeth can be pushed into the substratum; also, large stones and coarse gravel tend to wedge between the teeth and prevent the jaws closing. However, on small gravel, sand, silt, clay and mud it worked very efficiently, also weed beds can be sampled by cutting off and discarding the mass pulled up and remaining outside the jaws. The great advantage to the operator of knowing exactly where his grab is and what it is doing is apparent when an obstruction such as a sunken branch is struck in soft mud. The relative position of the two T grips shows at once whether the jaws are fully closed or not and, if necessary, the jaws can be opened and another attempt made without bringing the grab to the surface.

My thanks are due to my colleague, Mr A. Swain, for his assistance in the development of this grab, and to Mr W. J. Caulfield of 21 Sheldon Avenue, Barkingside, Ilford, Essex, who constructed the grab and to whom many improvements in the original design are due.

Pl. 3 shows the grab from various angles and in use on the River Nene, Northamptonshire.



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A grab for sampling river beds.

REVIEWS

MAMMALS IN NEW ZEALAND

K. A. Wodzicki (1950). *Introduced Mammals of New Zealand: An Ecological and Economic Survey.* Bull. Dep. Sci. Industr. Res., New Zealand, No. 98. Pp. x + 255; 50 text-figures and photographs. Wellington. Price 12*s.* 6*d.*

New Zealand is undergoing strange ecological changes under the impact of introduced animals and plants. The almost entire absence of land mammals in the islands when white men first arrived, the result of immensely long zoogeographical isolation, led to a great deal of deliberate introduction, chiefly of European species, but also eventually of forms from Asia, North America and Australia. At first the invaders were welcomed for food, sport or as reminders of the home country. But the author traces most interestingly the gradual shift of opinion towards one that is at the present time critical of further introductions, and concerned with the very serious reaction that many of the established species are having upon their environment. The events that are taking place ought to be of deep interest to ecologists, because they raise all manner of problems about the nature of control in populations, and the part played in the distribution and composition of vegetation types by animals whose presence is often just taken for granted by botanists, and whose activities in a more balanced ecosystem are underrated.

Dr Wodzicki, who came to New Zealand with a record of distinguished ecological work in Poland, made his first task the assembly of historical facts about the main species of mammals that were ecological problems. He gives a complete list of attempted and successful introductions, the earliest being by Maoris (Maori rat and dog), the next being by Captain Cook and early nineteenth-century settlers (dog, cat, brown and black rats, house-mouse, rabbit, cattle, sheep, goat, pig and horse), and the rest mostly following the enthusiastic period of liberations from the mid-nineteenth century to the first decade of this one. The present monograph is concerned with a selected group of twenty-nine species, and its method has been to assemble every possible kind of information about them, both scientific and historical, including replies to questionnaires sent to people like forest officers. The evidence on such population histories is bound to be rather uneven, and some of it not of first-class reliability; but the general impression left by this book is of a careful and industrious survey such as has not previously been available at all, except for a few of the species. Wherever the data could be got, this general survey is supported by figures, usually for catches rather than for actual populations, and by such data about reproduction and other biological features as exist. There are excellent maps of the known distribution of the species, and a certain number of good photographs illustrating the habitats.

Amongst species that are given especial attention are the Australian 'opossum' (a Phalangerid, *Trichosurus vulpecula*), which has now been in the country for nearly a hundred years. Like the rabbit, they are trapped for their skins, but are also destructive. The rabbit is one of the tremendous agricultural pests, although at the time this inquiry was started no map of their population distribution existed. The wild goat, wild pig and red deer are probably the most destructive, or at any rate ecologically important, wild species in the rest of the list. The author concludes that 'deer are a serious menace in almost any part of their New Zealand habitat'. They are particularly dangerous to the natural renewal of the bush, with the further toll of soil erosion that this leads to.

An extraordinary collection of ungulates is now established firmly and is difficult to control, let alone eradicate. Among them are chamois and tahr in the mountains of the South Island, fallow deer, Japanese deer, moose, some sambar, Virginia deer (chiefly on Stewart Island) and wapiti. Smaller mammals include wallabies, hedgehog, stoat, weasel, polecat, rats and mice, and the hare.

Although this book does not pretend to enter into a deep analysis of the ecology of any of these species of mammal, it gives an extremely clear and interesting account of their present status, and is informed by an ecological outlook. Intensive work under Dr Wodzicki, who is

in charge of the Animal Ecology Section of the Department of Scientific and Industrial Research has been in progress since the last War, and its results will be looked for with interest.

There is a good bibliography, and the book is well arranged, but there is no subject index.

C. ELTON

BRITISH HERPETOLOGY

Malcolm Smith (1951). *The British Amphibians and Reptiles.* Pp. xiv + 318; 56 plates (18 in colour); 88 text-figures. New Naturalist Series. London and Glasgow: Collins. Price 21*s.*

Dr Smith's book is one of the New Naturalist series, the aim of which is to interest the general reader in the wild life of Britain. Although Dr Smith is so well known for his systematic work, in this book he appears as an ecologist, and has been successful in combining the aim of his publishers with that of providing an up-to-date ecological account, including many of his own unpublished observations, of the group of animals he has chosen to study. The result is a book which is certainly not for the general reader alone, but is of scientific importance as well.

After an historical introduction, each species is described in turn. There is enough anatomical description, with clear and simple diagrams, to illuminate the text, but the main emphasis is on the life histories. These are well documented and make most interesting reading. Dr Smith frequently points out the gaps in our knowledge, and indeed, has a chapter on unsolved problems, which may serve to encourage some of his readers to undertake observations of their own. Field work on Amphibia is apt to be cold, wet and dark (we should not forget the bias which human preferences introduce into ecology), but with this book for encouragement, perhaps we can look for studies of territory and courtship in reptiles to compare with those on the more popular birds.

The book is freely illustrated with beautiful colour photographs and many other illustrations. The neat diagrams of the annual life cycles call for favourable comment.

Dr Smith has made unusually free use of literal quotations from his various authorities. When bare facts and figures are to be recorded, a paraphrase may be as good as the original, but the subject-matter of ecology is sometimes contained in narrative, and then nothing quite replaces the original words of the observer of what may have been an event without parallel in the literature. Lawyers know the value of the words of a first-hand witness, and so apparently, does Dr Smith. This practice might well be extended by other authors.

Few errors have been detected. On p. 103, 'sperm emission movement' does not quite convey the meaning that the movement in question was part of a chain of signals from the female toad to the male, indicating that eggs were about to emerge.

The quantitative aspects of ecology have, perhaps, not had enough weight given to them, by comparison with the qualitative observations. For example, the natterjack (*Bufo calamita*) is stated not to be 'particular in its choice of ponds like the common toad'. But it lays about the same number of eggs, and probably matures at the same age, so that its reproductive potential, and therefore its total mortality, must be about the same. Unless the adults fare better than those of *B. bufo*, a safer assumption would seem to be that the ponds, however odd it may seem to us, are quite good places for natterjacks. In other parts, too, stress is laid on the heavy toll taken of amphibian life by various enemies. In this, Dr Smith is following a well-established tradition, and common observation seems to bear him out. But although the data may not be as full as could be wished, there seems enough evidence on the reproductive potentials of Amphibia to show that their total mortalities are no higher than those of small mammals and birds. The prodigal and fecund frog is probably a myth, arising from the public way in which the frog and its tadpoles live and die.

Rana esculenta and *R. ridibunda* are stated (p. 130) to have a pre-spawning period, but the description of their behaviour does not suggest that they have according to the definition in the previous paragraph. With these species, which are 'protracted breeders', it may not be necessary to look further for an explanation of the dates at which various individuals breed than to the maturation of the gonads. But perhaps the reader might have been warned that such internal physiological rhythms are normally not nearly accurate enough to account for synchronous behaviour, even in homoiothermal animals, in which the biochemical processes do at least proceed under constant temperature. They are not available as explanations of the

sharply defined date of breeding of many individual specimens of *R. temporaria*, without making highly improbable assumptions on the physiology of maturation.

The inclusion of a chapter on parasites, by Dr H. A. Baylis and Mr R. S. J. Hawes, is unusual, but commendable. It may induce some readers to study host and parasite together, in the field, and much of interest might then result.

The price of the book makes it excellent value, and could obviously not have been fixed so low if the book had been produced for a smaller market.

R. MAXWELL SAVAGE

NEMATODE TAXONOMY

T. Goodey (1951). *Soil and Freshwater Nematodes.* Pp. xxvi + 390; 191 text-figures. London: Methuen. Price 45*s*.

The outstanding merit of Dr Goodey's book as a work of reference is that it brings together in one convenient focus all essential information about the known genera of soil and fresh-water nematodes. The style is clear and economical throughout, and the substance of the book is largely factual and non-controversial. By means of the definitions of genera and the line diagrams it is now possible to make a beginning of the identification of nematodes encountered in soil and fresh-water habitats without undue labour. In the past, free-living nematodes have been neglected by ecologists and zoologists in general, partly because of the diffuse and scattered nature of the literature. Dr Goodey's book removes this difficulty and paves the way for further advances in this field. The book begins with a brief introductory section on some of the methods used in collecting and preparing nematodes for microscopical examination and on the general structure of nematodes. The main body of the work is set out according to the system of Chitwood and Chitwood, in their *Introduction to Nematology*, except for the Order Tylenchida, which is based on the more recent classification of Gerald Thorne. Each genus is defined and an illustrated description of the type species or some other characteristic species is given. This is followed by an alphabetical list of other species in the genus with their synonyms and by brief comments on their bionomics. Dr Goodey indicates clearly the genera which he considers of uncertain systematic position, and those for which the definition is inadequate or otherwise unsatisfactory. He also draws attention to the genera in which the status of the various species requires revision. The work terminates with an appendix on hairworms (*Gordiidae*) and a short bibliography of the more important literature cited. The book is printed on austerity lines and the reproduction of the line diagrams fails to do justice to the original drawings. A more extended treatment of the introductory sections on technique and the general structure of nematodes would have enhanced the value of the work. These criticisms are small, however, when weighed against the value of the book as a whole, and some of them are criticisms of the present times rather than of the author. Dr Goodey is to be congratulated on this solid contribution to nematology.

F. G. W. JONES

MAN AND HIS SURROUNDINGS

A. W. Boyd (1951). *A Country Parish.* Pp. xvi + 278; 82 plates (34 in colour); 9 text-figures. New Naturalist Series. London: Collins. Price 21*s*.

H. J. Fleure (1951). *A Natural History of Man in Britain.* Pp. xviii + 349; 76 plates (38 in colour); 76 text-figures. New Naturalist Series. London: Collins. Price 21*s*.

Perhaps I expected too much, but I confess to finding Mr Boyd's book a little disappointing. His earlier chapters on the human side of the picture—history, trades, customs and man's influence on the fauna and flora are interesting and pleasantly written. The later chapters on the fauna and flora, in which I hoped to find some attempt at an ecological account of the restricted area with which the book is concerned, proved to be little more than annotated lists too detailed to be very readable and with little discussion of ecological relationships. The illustrations are well chosen, almost without exception well photographed, some outstandingly well, and better reproduced than in many of the volumes of this series. Unfortunately the editors have forgotten (what they discovered after publishing the first volume of the series)

that when the plates are scattered through the book without regard to the subject-matter it is necessary to give page numbers as well as plate numbers in referring to them, and this makes the book singularly tiresome to read.

Prof. Fleure begins with a masterly and completely fascinating Introduction in which he surveys the effects of geological and geographical influences on the first men to settle in these islands. Unfortunately this early promise is not quite fulfilled in the following chapters which deal with the history rather than the natural history of man in Britain up to the Norman conquest. The treatment is necessarily brief and therefore tends to lack the guiding thread of continuity which the reader who is not intimately acquainted with the details needs, both to enable him to see the picture in perspective and to hold his interest. With chapter 9 begins a series of chapters which deal with various aspects of man and the environment he has made for himself, and the interest of the ecologist revives. The ethnological origins of the people, their clothes, dwellings, villages and towns all come under review in this way, and each chapter contains unfamiliar facts or a novel way of looking at things. There follow chapters on church and castle, communications and transport, and finally on the population of these islands, which are necessarily brief and eclectic and tend in places to somewhat dogmatic statement, but form a fitting climax to a book which in parts at least is of considerable interest to the ecologist and is somewhat different in character from most of the volumes of this series. Lack of efficient editing is sadly evident in this book, where many of the text-figures are placed far away from the passages they illustrate (e.g. Fig. 29 on p. 114 to which reference is made on p. 108, and Fig. 31 on p. 124 which is mentioned on p. 106), and some are inadequately described (e.g. Figs. 24 and 25 which are not referred to in the text at all). There are also a number of page references which have not been corrected in page-proof.

In a series in which it is the avowed intention to make full use of illustration it seems a pity that this should not be better done, both by better selection of illustrations, better reproduction of those selected, and better correlation of text and text-figures. On the first point, Pl. 10 in Prof. Fleure's book is an example of one which seems inept, and several other books of the series give the impression that some of their plates were only put in because the photographs were available. Since colour blocks are expensive it would surely be better to have fewer colour plates and spend the money on better reproduction than say Pls. 12 and 19 in Prof. Fleure's book. One suspects that the black and white plates also fail to do justice to the originals in some cases, and here again I would rather see the money put into really good half-tones printed on art paper even if it meant having fewer pictures.

H. C. G.

BOOKS RECEIVED

The North American Buffalo. A critical study of the species in its wild state. By Frank Gilbert Roe. University of Toronto Press; London: Geoffrey Cumberlege. 1951. Price 90*s.*

Man and The Animal World. By Bernal R. Weimer. New York: John Wiley and Sons; London: Chapman and Hall. 1951. Price 40*s.*

Animal Evolution. A study of recent views of its causes. By G. S. Carter. London: Sidgwick and Jackson. 1951. Price 30*s.*

A General Zoology of the Invertebrates. By G. S. Carter. Third edition, revised throughout. London: Sidgwick and Jackson. 1951. Price 35*s.*

N.A.A.S. Quarterly Review, no. 13, autumn 1951. H.M. Stationery Office. 1951. Price 1*s.*

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1951

Income

	£ s. d.	£ s. d.
Subscriptions received (including arrears, and *less* Payments in advance):		
Members taking *Journal of Ecology* only	486 17 2	
Members taking *Journal of Animal Ecology* only ...	250 7 4	
Members taking both Journals	278 17 5	
Associates	1 17 6	
	1017 19 5	
Less reserve carried forward to 1952 for second part of *Journal of Ecology*	245 0 0	
	772 19 5	
Add reserve brought forward from 1950	149 10 0	
		922 9 5
Interest on Investments	115 10 0	
Interest on Deposit Account	2 7 10	
Interest on P.O. Savings Bank Account	71 8 0	
		189 5 10
Journal of Ecology, sales *less* cost		64 18 2
Journal of Ecology, Index to vols. 1–20: Sales	8 4 0	
less cost ...	1 6 5	
		6 17 7
		£1183 11 0

Journal of Ecology:

Sales: Vol. 39, no. 1	459 19 2
Back volumes and parts	690 7 0
Reprints of papers	48 4 8
	£1198 10 10

Journal of Animal Ecology:

Sales: Vol. 19, no. 2	335 18 11
Vol. 20, nos. 1 and 2	662 4 5
Back volumes and parts	705 19 4
Reprints of papers	109 0 5
	1813 3 1
Balance (see above, under Expenditure)	159 12 5
	£1972 15 6

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing and Stationery	28 17 0	
Meeting expenses	28 7 10	
Clerical assistance	24 0 0	
Audit Fee	12 12 0	
Postages	9 9 5	
Travelling	6 9 5	
Addressograph, Stencils, etc.	3 1 8	
Telephone	19 3	
Bank charges	10 8	
		114 7 3
Grants and Subscriptions:		
Freshwater Biological Association	10 0 0	
Biological Council Affiliation Fee	5 5 0	
British Co-ordinating Committee of I.U.P.N. ...	2 2 0	
		17 7 0
Journal of Animal Ecology: Costs *less* sales		159 12 5
Biological Flora of British Isles: Costs	32 5 11	
Less sales	30 17 9	
... ...		1 8 2
		292 14 10
Balance—Surplus for Year		890 16 2
		£1183 11 0

Journal of Ecology:

Costs: Paper, Printing, Plates, Binding	
Vol. 39, no.1	859 18 2
Publisher's Commission	141 0 7
Editorial expenses (including assistance) ...	87 0 3
Carriage, etc.	39 2 2
Insurance of Stock	4 0 0
Miscellaneous Expenses	2 11 6
	1133 12 8
Balance (see above under Income)	64 18 2
	£1198 10 10

Journal of Animal Ecology:

Costs: Printing, Paper, Plates, Binding	
Vol. 19, no. 2	519 13 1
Vol. 20, nos. 1 and 2	1140 1 4
Publisher's Commission	220 17 6
Carriage, etc.	52 18 9
Fee for checking references	20 0 0
Insurance of Stock	10 17 8
Editorial expenses	8 7 2
	£1972 15 6

BALANCE SHEET AT 31 DECEMBER 1951

Assets

	£ s. d.	£ s. d.
Cash in hand at Westminster Bank		
Current Account	428 3 4	
Deposit Account	200 0 0	
		628 3 4
Post Office Savings Bank Account		3052 10 8
Publishing Accounts due from the Cambridge University Press:		
Journal of Ecology	561 4 11	
Journal of Animal Ecology	832 14 5	
Biological Flora of the British Isles	23 13 9	
Journal of Ecology. Index, vols. 1–20	6 17 7	
		1424 10 8
Account paid in advance for Printing		3 3 1
Investments at Cost:		
£1200 of 3½% War Loan Stock	1230 4 1	
£700 of 3% Savings Bonds 1960/70	700 0 0	
£300 of 3% Savings Bonds 1965/75	300 0 0	
£1000 of 3% Redemption Stock 1986/96	1005 18 6	
		3236 2 7
		£8344 10 4

A further Asset, not valued, is the Unsold Stock of Journals, Index Volume, and *Biological Flora* Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
C. E. HUBBARD
Hon. Treasurers

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1952/55		29 11 3
Library Fund		1 5 0
Printing Accounts owing to Cambridge University Press:		
Journal of Animal Ecology		492 3 10
Sundry Accounts owing:		11 2 5
Reserve of Subscriptions for 1951 allocated to ... *Journal of Ecology* Vol. 39, no. 2		245 0 0
General Revenue Account—Surplus in hand:		
Balance at 31 December 1950...	6674 11 8	
Surplus for the year 1951	890 16 2	
		7565 7 10
		£8344 10 4

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants

120, BISHOPSGATE, E.C. 2
and
56, STATION ROAD, LOUGHTON, ESSEX.
18 *March* 1952